





KIRTLANDIA

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NUMBER 1

A NEW MARINE MEMBER IN THE CONEMAUGH GROUP OF OHIO

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ABSTRACT

A previously unreported marine limestone from the Conemaugh Group, Pennsylvanian, of Ohio is described as a new stratigraphic unit, the Noble Limestone Member. The type section is designated as the shale pit of the Ava Brick Co., in the SE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 31, Buffalo Twp., Noble Co., Ohio. The position of the new unit is between the Ewing and Rock Riffle Limestones. At two localities the Noble Limestone overlies a thin carbonaceous deposit and an underclay which may represent the Upper Bakerstown Coal and Clay. Fossils collected from the new member consist for the most part of bryozoans, brachiopods, and dissociated crinoid plates and stems. It is suggested that an unnamed marine shale that overlies the Upper Bakerstown Coal in the vicinity of Bakerstown, Pennsylvania may be the stratigraphic equivalent of the Noble Limestone.

A previously undescribed marine unit in the Conemaugh Group, Pennsylvanian, of Ohio was discovered in the spring of 1966 by Murphy and Mr. Harry Izenour of Salem, Ohio. The name Noble Limestone Member is here proposed for the new unit; the name is derived from Noble County, Ohio, where typical exposures of the new member occur. The type section is designated as the shale pit of the Ava Brick Company, in the SE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 31, Buffalo Twp., Noble County, Ohio. The measured section follows:

Pennsylvanian:	Ft	in
Conemaugh Group:		
Shale, buff, limonitic, thin-bedded, mostly covered, measured to highest float blocks of Ames Limestone -----	13	0
Harlem Coal and Clay: smut and underclay -----		6

Shale, maroon, weathers easily; contains fresh-water limestone nodules which probably represent the Rock Riffle Limestone, partly covered near top -----	9	0
Noble Limestone:		
Limestone, gray, nodular, thin-bedded, marine, brecciated near top, sparingly fossiliferous, non-persistent -----		4
Limestone, white to gray, weathers buff; nodular, marine, sparingly fossiliferous; interbedded with green to greenish-gray, dense, calcareous, fossiliferous marine shale -----	2	3
Clay shale, blue, nonfossiliferous -----	2	2
Shale, gray, with coal plant remains; probably represents the Upper Bakerstown Coal -----		3
Clay shale, yellow, finely laminated; may represent the Upper Bakerstown Underclay -----	1	9
Ewing Limestone: limestone, gray, nodular to thin-bedded, fresh-water, with abundant <i>Spirorbis</i> , small pelecypods, <i>Xenacanthus</i> , and other vertebrate remains; interbedded with mottled maroon shale containing hematite nodules -----	5	10
Cow Run Sandstone:		
Shale, mottled buff-green, massive; includes calcareous nodule layer with nodules up to 1 foot in diameter -----	13	0
Shale, mottled blue-brown, thin-bedded, with some calcareous nodules -----	4	6
Covered interval -----	20	0
Portersville Limestone and Shale: shale, black, laminated, calcareous, very fossiliferous limestone nodules; grades upward into blue to gray, finely laminated clay shale, sparingly fossiliferous, with nonfossiliferous lenticular limestone nodules; upper contact covered -----	13	9
Anderson Coal -----	1	4
Clay shale, gray to buff, slumped and partly covered; scattered limestone nodules near base probably represent the Bloomfield Limestone -----	6	5
Cambridge Limestone: limestone, mottled, maroon, gray, and green; marine, ferruginous, weathers dark brown -----		8
Covered interval -----	2	9

Another section exposing the units between the Ewing Limestone and the Ames Limestone is in south-central sec. 30, Buffalo Twp.

Pennsylvanian:

Conemaugh Group:	Ft	in
Ames Limestone -----	1	3
Shale and covered interval, including Harlem Coal float --	28	7
Noble Limestone: limestone, white, nodular; interbedded in olive clay shale, fossiliferous, marine; thin yellow clay, possibly representing the Upper Bakerstown Underclay, at base -----	1	3
Shale, mottled tan and buff -----	1	1
Shale, variegated, green and maroon, hematite nodules in upper third, carbonaceous near top -----	5	1
Ewing Limestone: limestone, irregularly bedded, fossil- iferous, fresh-water -----	8	3

The area between this section and the type section is very poorly exposed, and the Noble Limestone could not be located. Just north of the place of the second section, however, the interval in which the Noble Member would be expected to occur is occupied by tan, silty shale which contains plant fragments, estherids, and fresh-water pelecypods (*Anthraconaia* cf. *A. arenacea* (Dawson)). The Ewing Limestone is exposed along the road in south-central sec. 19 and along the highway in the SW $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 24, Buffalo Twp., Noble County, Ohio, but no marine fossils were found in the overlying shales.

The Ewing and Noble Limestones do not seem to be represented in adjoining parts of Spencer Township, Guernsey County, and Noble Township, Noble County, where the interval between the Ames and Portersville Limestones appears to consist for the most part of channel sandstones or channel sandstones and interbedded shales.

The Noble Limestone has been found at only one other locality, in the King Quarry at Florence, 1 mile north of Caldwell, Ohio. A measured section at this locality appears in Denton and others (1961, p. 194, section 11), although the Noble Limestone Member is not noted in this section. The limestone is present, however, at least in the northern portion of the quarry, where it ranges between four and five feet in thickness and consists of the usual fossiliferous, white to gray, nodular limestone interbedded with greenish fossiliferous shale. In an abandoned quarry just southeast of the King Quarry, marine fossils are absent at the top of the Ewing. In new

road cuts due west of the quarry, on the west side of Duck Creek, the Noble Limestone Member is absent.

A faunal list derived from collections made at the Ava Brick Company Shale Pit and the King Quarry is given below. Dr. Richard Hoare, Department of Geology, Bowling Green State University, and Mr. J. J. Burke, Cleveland Museum of Natural History, have been of considerable help in identifying several of the brachiopods and the crinoid material. These collections have been presented to the Cleveland Museum of Natural History.

Species	King Quarry	Ava Shale Pit
Anthozoa:		
<i>Stereostylus amesensis</i> Bebout	x	
Echinodermata:		
<i>Erisocrinus typus</i> (Meek and Worthen)		x
Crinoid fragments	x	x
Bryozoa:		
Unnamed solid ramose fistuliporid (Vide Moore and Dudley, 1944, p. 265)	x	
<i>Polypora</i> cf. <i>P. valida</i> Moore	x	x
<i>Septopora robusta</i> Ulrich	x	
<i>Megacanthopora</i> cf. <i>M. fallacis</i> Moore	x	
Brachiopoda:		
<i>Lingula carbonaria</i> Shumard		x
<i>Trigonoglossa nebrascensis</i> (Meek)		x
<i>Orbiculoidea missouriensis</i> (Shumard)		x
<i>Derbya crassa</i> (Meek and Hayden)	x	
<i>Chonetinella flemingi</i> (Norwood and Pratten)	x	x
<i>C. flemingi alata</i> (Dunbar and Condra)	x	x
<i>C. verneuilliana</i> (Norwood and Pratten)		x
<i>Juresania nebrascensis</i> (Owen)	x	x
<i>Pulchratia ovalis</i> (Dunbar and Condra)	x	x
<i>Antiquatonia portlockianus crassicosatus</i> (Norwood and Pratten)	x	x
<i>Linoproductus prattenianus</i> (Norwood and Pratten)		x
<i>Neospirifer dunbari</i> King	x	x
<i>Punctospirifer kentuckensis amesi</i> Hoare and Sturgeon Ms	x	x
<i>Crurithyris planconvexa</i> (Shumard)		x
<i>Composita subtilita</i> (Hall)	x	x
Pelecypoda:		
<i>Dunbarella</i> cf. <i>D. striata</i> (Stevens)		x
<i>Acanthopecten carboniferus</i> (Stevens)		x
Cirripedia:		
<i>Trypetesa caveata</i> Tomlinson	x	x

Vertebrata:

<i>Petalodus ohioensis</i> Safford	x	x
<i>Deltodus</i> sp.	x	

Certain elements of the Noble Limestone fauna have not been reported previously from Conemaugh beds older than the Ames Limestone. These include the coral *Stereostylus amesensis* Bebout, along with two brachiopods, *Pulchratia ovalis* (Dunbar and Condra) and *Punctospirifer kentuckensis amesi* Hoare and Sturgeon Ms. The unnamed solid fistuliporid bryozoan found in the Noble Limestone is of interest, for the only other large fistuliporids known from the Pennsylvanian of Ohio are specimens of *Cyclotrypa* that occur in the Ames Limestone. The presence of the forms cited above in the Noble Limestone indicates that the Noble fauna is trending toward that of the Ames and is more advanced in that direction than other Lower Conemaugh marine faunas. However, the chonetid brachiopod *Chonetinella*, which is characteristic of other Conemaugh marine limestones underlying the Ames, is common in the Noble fauna. This is in marked contrast with the fauna of the Ames, in which *Neochonetes* is the common and characteristic chonetid.

Unfortunately, present knowledge of the Conemaugh faunas is not refined enough to permit precise correlation of units over wide areas. The Portersville Limestone of Ohio has been correlated with the Woods Run Limestone of western Pennsylvania (Sturgeon and others, 1958, p. 118, 122; Flint, 1965, p. 70-71), but this has been done solely on the basis of its stratigraphic position. Burke (1958, p. 302) described three distinct marine members in the interval between the Cambridge and Ames members: Woods Run proper, the underlying Nadine Member, and the overlying Carnahan Run Shale; as a consequence there is considerable doubt about which particular unit corresponds to the Portersville Member.

The Noble Limestone definitely occurs above the Ewing Limestone, which is known to underlie the coal distinguished in Ohio as the Upper Bakerstown. The horizon of this coal appears to be indicated by smut and underclay underlying the Noble Limestone in the sections given above.

The coal which in western Pennsylvania is regarded as the Upper Bakerstown is found in the vicinity of Bakerstown, Allegheny County, Pennsylvania, and lies 50 to 60 feet below the Ames

Limestone. In the course of recent investigations we have discovered that a marine shale immediately overlies that coal in the vicinity of Bakerstown. The shale, carrying a predominately moluscan fauna, was found at two localities, one just west of the junction of Pennsylvania State Routes 8 and 910, 1.2 miles south of Bakerstown, and the other just east of the toll station at Interchange 4 on the Pennsylvania Turnpike, 2.9 miles south of Bakerstown. The presence of a marine shale overlying the Upper Bakerstown Coal in Pennsylvania, and apparently occupying the same stratigraphic position as the marine Noble Limestone of Ohio, strongly suggests that the two beds are correlative.

Burke (personal communication, September 1967) has found no conclusive evidence that the Upper Bakerstown Coal is present in his area of investigation in the Kiskiminetas Valley, and he is inclined to believe that in that area this coal should occur higher in the stratigraphic section than any of the marine beds underlying the Ames Limestone that he distinguished in 1958.

In summary, the Noble Limestone in Ohio represents a previously unrecognized marine unit that occurs in the interval between the Portersville and the Ames Limestones. However, more field study is required before the relationship of the Noble Limestone to various Conemaugh marine units in Pennsylvania can be determined.

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KIRTLANDIA

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NUMBER 2

PRELIMINARY DESCRIPTION OF A NEW GONIOPHOLID CROCODYLIAN

Charles C. Mook*

ABSTRACT

A goniopholid crocodile, *Eutretauranosuchus delfsi* n.g., n.sp. from the Morrison Formation, Jurassic, near Canon City, Colorado, is described. The new crocodilian is unique in showing a palatal opening anterior to the internal nares and medial to the palatal vacuities.

INTRODUCTION

In 1957, a party under the leadership of Edwin Delfs, M.D. collected fossil reptilian remains from the Morrison Formation near Canon City, Colorado. Included in this material was a fairly complete skeleton of a small crocodilian. This, along with other reptilian remains, is now in the collection of the Cleveland Museum of Natural History. When the crocodilian material was prepared, it was evident that it possessed goniopholid characters. Other characters that are unique indicated a new genus for which Dr. Delfs suggested the name *Eutretauranosuchus* signifying "doubly pierced palate"). The material was assigned to me for description. I wish to express my thanks for this privilege to Dr. Delfs and to the authorities of the Cleveland Museum.

The illustrations of the type are derived from photographs made by the Photographic Department of the American Museum of Natural History.

*Dr. Mook died in October, 1966, while this note was in press.

SYSTEMATIC DESCRIPTION

Order CROCODILIA

Suborder MESOSUCHIA

Family GONIOPHOLIDAE

Genus EUTRETAURANOSUCHUS, new genus.

Diagnostic characters: The skull is moderately long in proportion to its breadth. There is a pronounced depression at the base of the snout, and slightly developed preorbital ridges, suggesting the condition in the living caimans. The postorbital bars were clearly subdermal. The prefrontal bones extend farther forward than the frontal. The nasal bones widen anterior to the prefrontal tips. The nasal bones do not enter the external narial aperture at the surface. The frontal bone extends forward to the level of the eleventh maxillary teeth. The frontoparietal suture is located rather far back, permitting a considerable participation of the frontal in the anterior borders of the supratemporal fenestrae. The interfenestral bar is relatively broad and flat, and its edges are slightly uprolled. The supratemporal fenestrae are of moderate size. They are elongate oval in shape. The quadratojugal bones have sharp spines, resembling those of *Crocodylus*.

The internal narial aperture is unusually long and slender, its length being several times its breadth, and relatively much longer than in other crocodilians of its general size. It appears to be divided, at the palatal surface, at least, by a slender bar of bone. The composition of this bone is not clear, but it may be made of slender anterior processes of the pterygoid.

Anterior to the internal narial aperture is another opening, similar in character to it, but smaller. Like the internal nares it is divided by two slender bones, which appear to be processes of the palatines. The presence of this opening is unique among crocodilians.

The palatine fenestrae are large and are broad anteriorly. Their anterior ends lie opposite the eighteenth maxillary teeth. The pterygoid, omitting the anterior processes mentioned above, is short and broad. The palatine bones extend forward to the level of the thirteenth maxillary teeth.

The lower jaw is long, slender and unusually low anteriorly. The symphysis includes eight mandibular teeth on each side. The splenial bones enter the symphysis. They extend forward to the level of the seventh mandibular teeth.

Twenty-four alveoli are present in each ramus. Of these numbers 3 and 4 are slightly larger than the rest which are subequal in size. Numbers 1 and 2 appear to open on the external surface of the jaw. The first eighteen alveoli have separate walls, nineteen to twenty-four merge together. Numbers 5 to 11 are visible from the side. The external mandibular fenestrae are small and are oblique in position. They are much longer than high. The anterior internal fenestra is moderately large and the posterior one is small.

The articular process is excessively short and the articular surface, that articulated with the quadrate, is also very short.

The teeth, such as they are preserved, are rather small, are striated, and slightly bladed.

The posterior external portions of both rami are distinctly pitted, the anterior portions only slightly so.

The vertebrae are amphicoelous, and are goniopholid in character.

The limb bones are typically crocodilian and appear to be rather short for their breadth and in proportion to the dimensions of the skull and vertebrae.

Type: *Eutretauranosuchus delfsi* Mook.

Eutretauranosuchus delfsi, new species

Type: Well-preserved skull and jaw; most of the precaudal and a few caudal vertebrae; a few limb bones; scutes; Cleveland Museum of Natural History, No. 8028.

Type locality and level: Red Canyon, north of Canon City, Colorado; lower level of the Morrison Formation, upper Jurassic.

Diagnostic characters: As for the genus, of which this species is the sole representative.

The name is given in honor of Dr. Edwin Delfs in recognition of his services to paleontology in the discovery of this and other specimens of fossil reptiles in the Canon City area.

MEASUREMENTS

SKULL:

	mm
Length, tip of snout—occipital condyle	218 est.
Length, tip of snout—posterior border of cranial table	207 est.
Length, base of snout—occipital condyle	88
Length, base of snout—posterior border of cranial table	80
Breadth across base of snout	76
Breadth across quadratojugals	108
Breadth across cranial table, anterior end	61
Breadth across cranial table, posterior end	68
Length of right orbit	22.5
Breadth of right orbit	16
Length of left orbit	24
Breadth of left orbit	18
Length of right supratemporal fenestra	25
Breadth of right supratemporal fenestra	14
Length of left supratemporal fenestra	27
Breadth of left supratemporal fenestra	15
Length of right palatine fenestra	43
Breadth of right palatine fenestra	24
Length of left palatine fenestra	43
Breadth of left palatine fenestra	27
Breadth across pterygoids	85

LOWER JAW:

	<i>Right ramus mm</i>	<i>Left ramus mm</i>	<i>Both rami together mm</i>
Length, total	256	261	-----
Length, tip—posterior end of tooth row	159	-----	-----
Length, posterior end of tooth row— end of articulae	111	-----	-----
Length, symphysis	54	53	-----
Length, external mandibular fenestra	35	38	-----
Length, articular (articulating surface plus process)	39	37.5	-----
Height, external mandibular fenestra	11	9	-----
Breadth across symphysis	-----	-----	28

COMMENTS

The characters of the palate present a considerable departure from the condition usually seen in mesosuchian crocodiles. The very large internal narial aperture, together with the anterior opening, which must have entered the narial passage are unique. They indicate specialization among the goniopholids comparable to the wide range of specializations that may be noted among the Crocodilidae in the Eusuchia.

MANUSCRIPT RECEIVED MARCH 6, 1965

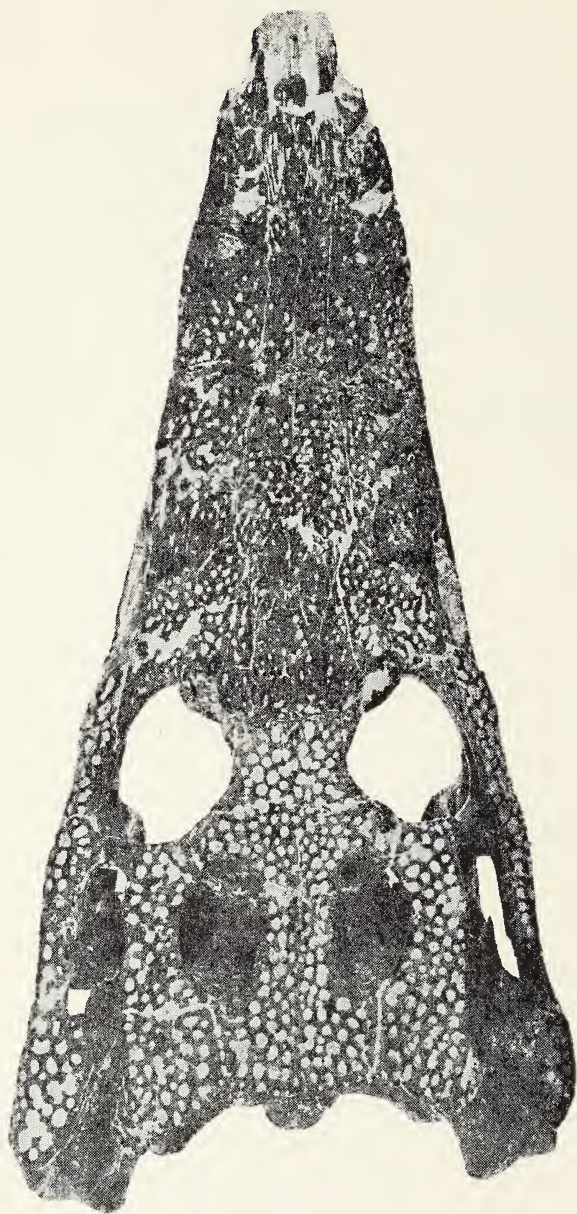


Plate 1. *Eutretauranosuchus delfsi* n.gen., n.sp. Type, skull, C.M.N.H. No. 8028. Superior view. Two-thirds natural size.



Plate 2. *Eutretauranosuchus delfsi* n.gen., n.sp. Type, skull, C.M.N.H. No. 8028. Inferior view. Two-thirds natural size.



Plate 3. *Eutretauranosuchus delfsi* n.gen., n.sp. Type, lower jaw, C.M.N.H. No. 8028. Superior view of the two rami, not joined together. Two-thirds natural size.



Plate 4. *Eutretauranosuchus delfsi* n.gen., n.sp. Type, lower jaw, C.M.N.H. No. 8028. Upper figure: left ramus, external view; lower figure: right ramus, external view. Two-thirds natural size.



Plate 5. *Eutretauranosuchus delphi* n.gen., n.sp. Type, lower jaw, C.M.N.H. No. 8028. Upper figure: left ramus, internal view; lower figure: right ramus, internal view. Two-thirds natural size.

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KIRTLANDIA

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PACHYLOCRINIDS FROM THE CONEMAUGH GROUP, PENNSYLVANIAN

J. J. Burke

ABSTRACT

Four new species of pachylocrinid inadunate crinoids from the Conemaugh Group, Pennsylvanian, are described and attributed to the genus *Plummericrinus*. Three of these forms, *P. monongaliensis* sp. nov., presumably from the Brush Creek Limestone, Monongalia County, West Virginia, *P. emilyae* sp. nov., from the Ames Limestone, Carroll County, Ohio, and *P. pittsburghensis* sp. nov. from the Ames Limestone, Allegheny County, Pennsylvania, have dorsal cups with slight interrational notches, pits at the corners of the cup plates, and generally resemble *P. colubrosus* (Moore) although the cups are bowl-shaped rather than subpyriform; a fourth species, *P. nettingi* sp. nov., from the Cambridge Limestone, Allegheny County, Pennsylvania, has a truncate cone-shaped cup, prominent interrational notches and the characteristic splay-toothed outline of *P. mcguiri* (Moore).

The presence, in *P. monongaliensis* sp. nov., of muscular articulations connecting anal X and the right tube plate with the two tube plates overlying them is taken to indicate that some flexion of the anal tube was possible in this and other pachylocrinid species where similar articulations characterize these anal plates.

Four new species of pachylocrinid inadunate crinoids are described in the present paper and attributed to the genus *Plummericrinus*. The specimens on which the descriptions are based are from the Conemaugh Group, Upper Pennsylvanian, of Ohio, West Virginia and Pennsylvania. In addition to material from the Cleveland Museum of Natural History, specimens described herein or used for comparative study were borrowed from the Carnegie Museum and the United States National Museum. I am grateful to the authorities of these institutions for permission to study and to describe these specimens.

I wish to acknowledge the assistance of Mr. Bruce Frumker for photography, and my wife, Emily, for arranging the illustrations.



SYSTEMATIC PALEONTOLOGY

Family PACHYLOCRINIDAE Kirk, 1942

Genus **PLUMMERICRINUS** Moore and Laudon, 1943**PLUMMERICRINUS MONONGALIENSIS**¹ sp. nov.

Fig. 1

Diagnosis: Dorsal cup about as wide as that of *Plummericrinus colubrosus* (Moore) but higher (form ratio .54) and bowl-shaped, rather than subpyriform; walls of basal concavity less steep, infra-basals and basals less reduced. Interradial notches slight, pits at corners of cup plates, radialian strongly reduced, brachials without keels.

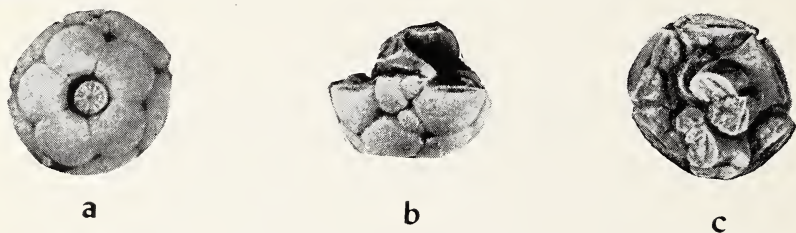


FIG. 1. *Plummericrinus monongaliensis* sp. nov. Holotype, a dorsal cup, U.S.N.M. no. 27488, from the ?Brush Creek Limestone, Conemaugh Group, Monongalia County, West Virginia. a, dorsal view; b, posterior view; c, ventral view, $\times 3$.

Holotype: U.S. National Museum no. 27488, a dorsal cup with first two primibrachs (B and C rays) and first two secundibrachs (B ray).

Occurrence: ?Brush Creek Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Monongalia County, West Virginia.

Repository: United States National Museum, Washington, D.C.

Description: The dorsal cup of this species is truncate bowl-shaped; the outline in dorsal and ventral view is subround and asymmetrical because the plates of the posterior interradius and the right posterior radial bulge outward to some extent. There is a distinct basal impression, which is relatively deep for *Plummericrinus*; its diameter is about one-third that of the cup. The proximal portion of the round stem is preserved; the articular surface of one colum-

¹ Named for Monongalia County, West Virginia.

nal shows 14 culmina and a subpentagonal lumen. The infrabasals extend beyond the stem, flaring downward steeply to meet the basals. The basals participate in the basal concavity and are strongly curved proximally; beyond the basal plane they are rather gently convex both longitudinally and transversely. These plates are only slightly wider than high, and are not impressed along their common sutures, but gentle furrows mark the sutures between the basals and the radials. At the tips of the radials and the basals there are definite deep pits at the plate junctions.

The radial plates are about a third wider than high. They are more convex longitudinally than transversely, but not strongly convex in any case. The furrows along the interrarial sutures are stronger than those along the radial-basal sutures, however. There are definite but not pronounced interrarial notches at the summits of these plates.

The radial articular surface is nearly as wide as the radial plate, although the transverse ridge is not. In lateral view, the outer marginal ridge sags downward with a gentle arcuate curve. In ventral view, the ridge has a stronger arcuate outline and bounds a relatively deep outer ligament area. The marginal ridge is not sharply delimited from the adjacent ligament area, which is denticulate. The ligament pit furrow is slitlike and not strongly excavated; the ligament pit is also slitlike. The transverse ridge is distinct and not denticulate. The inner ligament area is somewhat deeper than the outer. The oblique fossae are prominent, and a wide intermuscular notch separates the two triangular muscle areas, which face outward strongly.

Three plates occupy the posterior interrarial area. Pits and furrows mark their junctions *inter se* and with adjoining basals and radials. Of these plates, anal X is the largest. The radianal is about half the size of anal X, and the right tube plate is about one-third as large as anal X. Anal X abuts against the left posterior radial and rests on the truncated tip of the posterior basal and the upper side of the radianal. Below the right tube plate it makes contact with the right posterior radial; above that place the triangular right tube plate is wedged between anal X and the right posterior radial. The radianal is an elongate triangle; below its contact with anal X it is obliquely disposed between the posterior basal and the right posterior radial; it narrows to a tip and barely contacts the right posterior basal below. There is a distinct pit shared by the four plates

at this place of contact. Between the anal X and the posterior basal, there is a deep furrow, rather than a pit, and there is also a furrow marking the contact between anal X and the right posterior radial. Both anal X and the right tube plate extend only slightly higher than the summits of the radials and their distal articular surfaces lie in the same plane. Both plates resemble the radials in having external ligament furrows and pits, but the furrows and pits are less slitlike. These plates also exhibit transverse ridges and broad flat internal ligament areas.

The primibrachs of the B and C rays are present. They are wider than high, do not have median keels, and are axillary. The axillary face of the B ray primibrach is showing; it is divided by a median ridge into two articular surfaces, one for each first secundibrach. Each of these articular surfaces is composed of inner and outer ligament areas separated by a transverse ridge. The outer ligament areas are denticulate; the outer ligament pits lie within furrows. The two first secundibrachs of the C ray are also preserved. They are a little wider than high and nonaxillary. The upper articular surfaces show definite transverse ridges and inner and outer ligament areas resembling those of the radials. The outer ligament areas show denticulation.

Very fine granulose ornamentation is visible on the cup and brachial plates at a magnification of $20\times$.

Discussion: It is of interest to note that in this species the distal surfaces of anal X and the right tube plate are in essentially the same plane. Strimple (1961, p. 98) noted that in *Haerteocrinus*, *Texacrinus*, and *Plummericrinus* there is a trend toward this arrangement of these plates. Strimple has noted also (1952, p. 246) that in *Haerteocrinus turbinatus* "The upper surfaces of both RX and X have muscular fossae somewhat comparable to those of the RR. There is an outer ligament pit bordered by a transverse ridge. The outer marginal ridge and transverse ridge possess denticles, and other crenulations are found behind the muscle scar. Intermuscular notches are narrow and well defined, that of anal X being to the left of center, and of RX to the right of center."

This description in general applies to the facets of these anal plates in *P. monongaliensis* also. Furthermore, I have removed the matrix from the distal facets of these plates in the holotype of *P. mcguiri* (U.S.N.M. no. 141074); they show the same structures

noted by Strimple and the visible portion of the proximal facet of the large tube plate that succeeds anal X has a similar articular surface. A succeeding tube plate partly covers the distal surfaces of anal X and the right tube plate in the holotype of *P. colubrosus* (U.S.N.M. no. 141091) and I have not been able to make full preparation of the articular structures, but it is evident that they are much like those shown in *P. mcguiri*. In both of these Permian species the distal articular surfaces of anal X and the right tube plate are in approximately the same plane, as in *P. monongaliensis*. It is also worth noting that the largest plates of the tegminal sacs of *P. mcguiri* and *P. colubrosus* are in two rows, initiating with anal X and the right tube plate.

It appears evident that in some species of *Haerteocrinus*, *Texacrinus* and *Plummericrinus*, anal X and the right tube plate were joined to the two tube plates distal to them by muscular articulation. Furthermore, because in certain of these species the distal articular surfaces of anal X and the right tube plate are in the same plane, it is obvious that these two plates formed a common hinge with the proximal articular surfaces of the two tube plates immediately overlying them.

Because these anal plates were connected by muscular union of the same type as that which connected the arm plates of these species, it follows that some movement of the anal tube must have been possible—approaching, at least, that which was attained by the arms. In the case of *Plummericrinus* this is of special interest. Moore (1939, p. 221), because of the proximal location of what appeared to be the anal vent in *P. colubrosus*, stated that “this suggests that the main part of the tube functions mainly in connection with respiration or the water circulatory system rather than as covering for an elongated convoluted gut.” Possibly, if such were the case, movement of the tube contributed in some way to respiration or circulation of water.

Muscular articulation of this type is confined to the opposed faces of these pairs of anal plates of the anal tube in *P. mcguiri*, at least. In making further preparation of the holotype specimen of that species I uncovered two small plates of a row which originates at the left distal corner of the tube plate which overlies anal X. However, most of the distal surface of the latter tube plate articulated with a second large plate above, to the right of which I exposed another large plate which articulated with the plate which

rested above the right tube plate. Of these additional plates, all of the articular faces that are showing have moderate to deep fossae, with rims which, on the external side, at least, are crenulated. This type of articulation is usually interpreted as ligamentary. However, this does not rule out the possibility that contractile fibers might have been present, which would have contributed to flexion of the tube.

Of the anal plates within the dorsal cup of *Plummericrinus monongaliensis*, both anal X and the radianal are reduced, although anal X is still functional, as indicated by the articular surface noted previously. The separation of anal X from the radianal is unusual. I have not seen this condition in any other specimen of *Plummericrinus*. It may be only a simple case of variation and not characteristic of the species. However, coupled with the reduction of the radianal, it suggests that in this species we may be dealing with a trend toward loss of the radianal through resorption.

The specific locality and horizon from which this excellent little specimen was taken cannot be determined with certainty. I found it in the fossil crinoid collection of the United States National Museum. It is identified on the original handwritten label as "*Hydreionocrinus discus* (Meek & W.)" by "C.S." with the notation "Upper Carb./locality lost." Another label (typewritten) gives the same information but adds "Found among Monongalia Co., W.Va. fossils (C.S.)." I gather that the "C.S." refers to Charles Schuchert.

It appears quite likely that this dorsal cup is the specimen noted as "*Erisocrinus*, undetermined species" by Meek (1871) in a list of fossils reported by Stevenson (1871) to have been taken from the Uffington Shale, Conemaugh Group, near Morgantown, W.Va. The fossils listed were embodied in the United States National Museum collection, but many of them cannot be found at the present time. It has since been determined (Price, 1917; Murphy, 1966) and from my own field observations, that the Uffington Shale in the Morgantown area does not carry a marine fauna, and that the fossils identified by Meek probably came from the Brush Creek Limestone. It was my impression, in the course of preparation of the holotype of *Plummericrinus monongaliensis* that the matrix adhering to the specimen was characteristic of the Brush Creek, and Mr. James Murphy, who has collected marine fossils from the Brush Creek in the Morgantown area, is of the same opinion (personal communication, Feb. 16, 1968).

Linear measurements of the holotype, in millimeters, are given below:

Height of dorsal cup	3.7
Greatest width of cup	6.9
Ratio of height to width	0.54
Height of basal concavity	0.6
Width of basal concavity	2.3
Width of infrabasal circlet	1.9
Height of basal (raB)	2.6
Width of basal (raB)	2.8
Height of radial (aR)	2.3
Width of radial (aR)	3.5
Width of transverse ridge (aR)	3.3
Length of suture between basals	1.5
Length of suture between radials	1.1
Height of radianal	1.3
Width of radianal	1.3
Height of anal X	1.5
Width of anal X	1.3
Height of right tube plate	0.9
Width of right tube plate	0.8
Height of first primibrach (C ray)	2.3*
Width of first primibrach (B ray)	3.1
Height of first secundibrach (B ray)	2.0
Width of first secundibrach (B ray)	2.2

* Approximate

PLUMMERICRINUS NETTINGI² sp. nov.

Fig. 2

Diagnosis: Dorsal cup resembling that of *Plummericrinus mcguiri* (Moore) in having prominent interradianal notches, outflaring radials and lacking pits at corners of plates, but differing in smaller size (width 13.8 mm) and in tending toward truncate-cone shape, with shallower basal concavity and less elongate basals and radials.

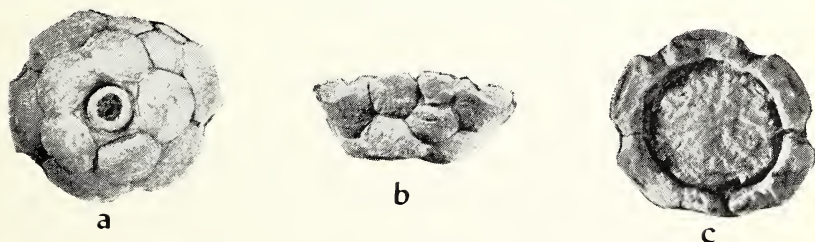


FIG. 2. *Plummericrinus nettingi* sp. nov. Holotype, a dorsal cup, Carnegie Museum no. 29857, from the Cambridge Limestone, Conemaugh Group, near Verona, Allegheny County, Pennsylvania. a, dorsal view; b, posterior view; c, ventral view, $\times 2$.

² Named for Dr. M. Graham Netting, Director, Carnegie Museum.

Holotype: Carnegie Museum no. 29857, a dorsal cup.

Occurrence: Cambridge Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Sylvan Run, near Verona, Allegheny County, Pa. (Lat 40° 29' 25" N, Long 79° 50' 50" W).

Repository: Carnegie Museum, Pittsburgh, Pa.

Description: The dorsal cup of this crinoid is modified truncate cone-shaped. In dorsal view the rounded outline of the basal circlet is in marked contrast with the scalloped outline of the radial circlet resulting from prominent interrarial notches at the summits of the outflaring radial plates.

The outer ring of one columnal of the round stem is preserved and shows faint traces of culmina. The basal concavity is distinct. The width of the concavity is less than one-third that of the cup, but the height is only about one-seventh of the cup height.

The infrabasals are relatively prominent, with tips extending well beyond the stem. These plates are slightly convex and slope downward gently to meet with the basals.

The basals participate in the basal concavity and are sharply convex longitudinally in that region. Beyond the concavity the basals are moderately convex. These plates are almost a fifth wider than high. There are gentle furrows along the sutures between the basals, and distally the tips of the basals are sharply incurved to meet the interrarial sutures.

The radials are about half as high as wide and flare outward strongly in the midregion, where they show little curvature. Along the sides, however, they are distinctly incurved, producing distinct hollows that border the interrarial sutures. There are prominent interrarial notches, with broad slopes, and the articular surface does not occupy the full width of the radial.

In general, the radial articular surfaces are not strongly developed and they are not well defined. The outer ligament area may be described as deep, although less so than the inner ligament area. The outer marginal ridge is arcuate, and the ligament area is denticulate. The ligament-pit furrow is slitlike, but I cannot distinguish a distinct ligament pit. There is a fairly strong transverse ridge, which is not denticulate. The inner ligament area displays moderate oblique fossae and outward-facing muscle areas, sepa-

rated by a broad intermuscular notch. There are also traces of the intermuscular furrow.

The radianal is the largest plate of the posterior interradius. Proximally it is wedged in between the posterior basal and the right posterior basal. Laterally it contacts anal X on the left and the right posterior radial on the right. Distally it bears the right tube plate, which intervenes between the right posterior radial and anal X. Anal X is somewhat smaller than the radianal; in addition to its contacts with the radianal and the right tube plate it rests on the truncate tip of the posterior basal below and also abuts against the left posterior radial on the left. The right tube plate is much smaller than the other two anal plates. The superior surfaces of anal X and the right tube plate are damaged and I cannot determine their original structure. The right tube plate is somewhat out of place and overrides the underlying radianal slightly. Probably the superior surfaces of anal X and the right tube plate were in essentially the same plane.

The ornamentation consists of small irregular pustules, visible at a magnification of $10\times$. It appears to have been absent from the infrabasals and proximal portions of the basals.

Discussion: As the diagnosis indicates, this form is quite distinct from the other Conemaugh species described in this paper, particularly in showing strong interrarial notches and outflaring radial plates. In these respects it resembles the Permian *Plummericrinus mcguiri* (Moore), although differing from that species in its smaller size, different shape of the dorsal cup, shallower basal concavity and less elongate basals and radials. However, none of these characteristics would appear to bar it from the ancestry of the Permian species.

Linear measurements of the holotype, in millimeters, are as follows:

Height of dorsal cup	5.4
Greatest width of cup	13.8
Ratio of height to width	0.39
Height of basal concavity	0.8
Width of basal concavity	4.2
Width of infrabasal circlet	4.4
Height of basal (raB)	3.6
Width of basal (raB)	4.7
Height of radial (aR)	3.4
Width of radial (aR)	6.0
Width of transverse ridge (aR)	4.8
Length of suture between basals	1.7

Length of suture between radials	2.2
Height of radianal	4.0*
Width of radianal	3.7
Height of anal X	3.0
Width of anal X	3.4
Height of right tube plate	1.9
Width of right tube plate	2.5

* Estimated

PLUMMERICRINUS EMILYAE³ sp. nov.

Fig. 3

Diagnosis: A species resembling *Plummericrinus colubrosus* (Moore) in showing slight development of interradianal notches and in having pits at corners of cup plates, but a larger form (estimated crown height 34 mm, width of dorsal cup about 10 mm) having cup more bowl-shaped and basal concavity quite shallow, infra-basals and basals less reduced, summits of anal X and right tube plate not in same plane and keels of brachials absent or insignificant.

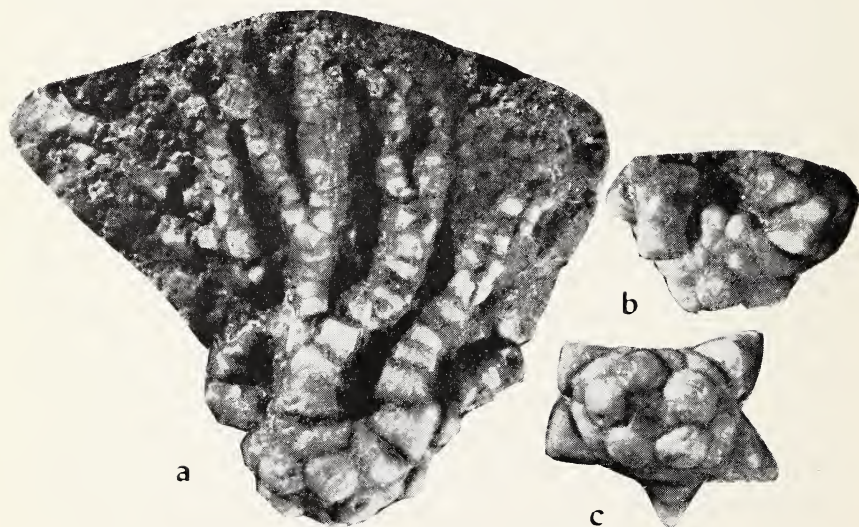


FIG. 3. *Plummericrinus emilyae* sp. nov. Holotype, a dorsal cup with portions of the arms attached, Cleveland Museum no. 4000, from the Ames Limestone, Conemaugh Group, about 3 miles east of Carrollton, Carroll County, Ohio. a, anterior view; b, posterior view; c, dorsal view, $\times 2$.

³ Named for my wife, Emily G. Burke.

Holotype: Cleveland Museum no. 4000, a dorsal cup with portions of the arms attached.

Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Joe Skinner Quarry, NW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 13 (Lat 40° 34' 20" N, Long 81° 01' 20" W) Center Township, about 3 miles east of Carrollton, Carroll County, Ohio.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

Description: Unfortunately, this specimen is contained in a very adherent matrix, and despite reasonable care in preparation, the component plates of the crown suffered some abrasion, although not to the extent that most of the salient characteristics were destroyed.

None of the arms is complete, but by conservative estimate the height of the crown was at least seven times that of the dorsal cup. The dorsal cup is truncate bowl-shaped. The stem is not preserved. Although the base of the cup has been abraded, it is evident that there is a distinct basal impression, the width of which is slightly more than one-third of the width of the cup; however, the maximum height of the impression, at most, is somewhat less than one millimeter. The stem impression is relatively small, a little less than a third as wide as the infrabasal circlet, consequently the infrabasal plates extended well beyond the stem. The greatest height of the basal impression is in the vicinity of junction of the infrabasal and basal plates; the stem impression does not extend to the basal plane of the cup, but the infrabasals flare upward slightly to meet the basals, and most of the wall of the impression is formed by the proximal portions of the basals.

The basal plates are a little more than one-fifth higher than wide. The left posterior appears to retain approximately its original slopes. Proximally, these plates show strong upward curvature, forming the walls of the basal impression. Distally, the longitudinal curvature is less pronounced; laterally, especially in the area between the basal sutures, the curvature is again strong, although somewhat less so than in the proximal region. These slopes form hollows bordering the basal sutures; there are also hollows, although generally broader, between the basals and the radials.

Apparently there were pits at all the angles where the basals meet with the radials and the anal plates, but traces of some of them have been obliterated.

The radials are nearly twice as high as wide. In general they tend to flare outward, their slopes diverging somewhat from those of the basals, although the tendency is not pronounced. These plates for the most part are nearly as convex as the basals along their height and are moderately convex transversely. Distally they curve inward strongly along a lunate area that sags downward from the summit corners of the plates; a similar upward arching area shows in the proximal portion of the primibrachs, consequently the sutures between the radials and the primibrachs are gaping. Interradial notches are present, but they are very slight. Except for the left anterior radial, which shows a trace of the outer ligament pit, details of the articular surfaces are concealed because the first primibrachs are all preserved.

The radianal plate is the largest of the anal plates; the right and left plates are somewhat smaller and anal X is slightly smaller than any of the others. The radianal extends proximally to the suture between the right posterior basal and the posterior basal. It abuts by a short side against the right posterior basal; a longer side borders the right posterior radial, and another long side rests against the posterior basal. A shorter side on the left contacts anal X. Above, the radianal supports the right tube plate, which fits in between the right posterior radial and anal X. The right tube plate extends for about half its height above the summit of the right posterior radial; on the left, above anal X, it rests against the left tube plate. Anal X rests on the truncate tip of the posterior basal below, and for most of its height contacts the left posterior radial, although it extends slightly above the summit of that plate. Above, it supports the left tube plate.

The first primibrachs of the A and C rays are higher than wide; those of the other rays are wider than high. These plates were abraded in preparation, but some of them now show sharp ridges along the midline that may be traces of keels. These plates are axillary. The right division of the A ray is complete to a short distance beyond the third isotomous division of the inner branch. There are six secundibrachs; the sixth is axillary. Ten tertibrachs are preserved in the outer ray and no evidence of branching. However,

the inner ray shows nine tertibrachs and the ninth is axillary. Four quartibrachs remain on one side following the bifurcation, one on the other. On the inner branch of the left division of the A ray, both first quartibrachs are preserved, resting on the axillary tertibrach. I find no evidence of tertiary division in either of the outer branches of the A ray.

A few slender pinnules are showing along the sides of some of the arms.

Discussion: This specimen is of interest because it shows the arm structure of the species, at least in part. Branching takes place on the first primibrach and again on the sixth secundibrach or thereabouts. From this point on there is no indication, from what is showing, of any further bifurcation on the outer branches, but the inner branches bifurcate again at the ninth tertibrach, as shown in one branch at least. This type of arm structure also characterizes *Texacrinus*, wherein, because the outer branches fail to show further bifurcation, the structure is termed exotomous. However, no species of *Plummericrinus* of which I know differs from *Texacrinus* in this respect, that is, they do not show any further bifurcation of these outer branches, so exotomous arm structure does not constitute a valid generic distinction between *Texacrinus* and *Plummericrinus*.

As a matter of fact, generic distinction between *Texacrinus* and *Plummericrinus* finds little support when based on other characters as well. Moore (1940, p. 144) cited the absence of interradianal notches in the holotype of *Texacrinus gracilis*, but the presence or absence of these notches is not regarded as a generic character in other inadunate crinoids; *Plaxocrinus*, for example, is composed of species some of which exhibit the notches, whereas others do not. The interposition of the radianal between the posterior basal and anal X appears to have been regarded as a generic character of *Texacrinus* by Strimple (1961, p. 94). However, variations in the arrangement of these anal plates will quite likely be found in species of *Texacrinus*. As regards *Plummericrinus*, the radianal separates anal X from the posterior basal in the holotype of *P. bellirugosus*. It is also interesting to note that in four paratypes of *P. mcguiri*, Moore (1939, p. 209) found the radianal separating anal X from the posterior basal.

The slight basal impression shown in *P. emilyae* constitutes at best a specific distinction that points up the transition in this respect from genera such as *Haerteocrinus*, in which the impression is lacking. Of more significance, it seems to me, is the fact that in *P. emilyae* the distal surfaces of anal X and the right tube plate are not in the same plane. In this respect *P. emilyae* appears to differ from most, if not all, other species of *Plummericrinus*.

Linear measurements of the holotype, in millimeters, are given in the following tabulation:

Height of crown	34.0*
Height of dorsal cup	4.9**
Greatest width of cup	10.1**
Height of basal concavity	0.7**
Width of basal concavity	3.7
Diameter of stem impression	1.0**
Width of infrabasal circlet	3.2
Height of basal (laB)	4.4
Width of basal	3.7
Height of radial (laR)	2.5
Width of radial (laR)	4.8
Length of suture between basals	1.6
Length of suture between radials	1.4
Height of radianal	2.3
Width of radianal	2.3
Height of anal X	1.8
Width of anal X	1.8
Height of right tube plate	2.0
Width of right tube plate	2.0
Height of left tube plate	2.0
Width of left tube plate	2.0
Height of first primibach (A ray)	4.3
Width of first primibach (A ray)	4.2
Height of first secundibrach (A ray)	2.8
Width of first secundibrach (A ray)	2.5
Height of first tertibrach (A ray)	1.5
Width of first tertibrach (A ray)	1.6

* Estimated

** Approximate

PLUMMERICRINUS PITTSBURGHENSIS⁴ sp. nov.**Fig. 4**

Diagnosis: Dorsal cup truncate bowl-shaped, estimated width 15 mm; interrarial notches slight, pits at corners of plates; plates only moderately convex; basals, radianal and anal X relatively large; posterior basal makes narrow contact with anal X; primibrachs without keels.

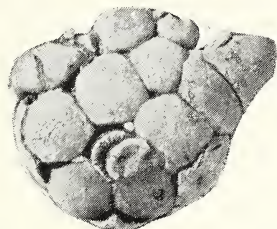


FIG. 4. *Plummericrinus pittsburghensis* sp. nov. Holotype, an obliquely crushed dorsal cup, Carnegie Museum no. 29858, from the Ames Limestone, Conemaugh Group, Brilliant Cutoff, Pittsburgh, Allegheny County, Pennsylvania. Dorsal view, $\times 2$.

Holotype: Carnegie Museum no. 29858, a dorsal cup with primibrachs of the C and D rays attached.

Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Brilliant Cutoff (Lat $40^{\circ} 29' N$, Long $79^{\circ} 54' 20'' W$) Pittsburgh, Allegheny County, Pennsylvania.

Description: Although the dorsal cup of the type has undergone compression, which makes it extremely difficult to determine the original outlines and dimensions, the specimen nevertheless preserves many characters which mark it as a representative of a distinct species.

The dorsal cup was apparently truncate bowl-shaped. There is a distinct basal concavity, the width of which, by rough estimate, was about one-fifth that of the cup. The depth of the concavity cannot be determined because portions of the stem are still in place. Three columnals and part of a fourth are showing; the columnals are thin, and each is estimated to bear about 35 culmina.

⁴ Named for Pittsburgh, Pennsylvania.

The infrabasals project slightly beyond the stem, and slope steeply downward. The circlet is evidently somewhat displaced in the present specimen, but the tip of one of the plates appears to be nearly in its original place, indicating that the plate leveled off distally into a triangular area that fitted in between adjacent basals.

Evidently the only participation of the basals in the basal concavity was in the form of a sharp curvature of their proximal portions that contributed to form a slight part of the wall of the concavity. Despite compaction, it is apparent that the slopes of the basal circlet were fairly gentle. The basal plates are a little wider than long, and are relatively large. In general they are moderately convex, although there are broad hollows bordering the basal sutures, and deep pits at the angles where they meet the radials, the radianal, and anal X.

It is difficult to estimate the original slopes of the radials, but from all appearances they did not deviate sharply from those of the basals, and this would have made for a bowl-shaped cup. The radials are gently convex longitudinally and transversely. These plates are about two-fifths wider than long. The interradianal notches are slight. Details of the articular surfaces are poorly preserved because of wear. The outer ligament area was apparently shallow in comparison with the inner area, and bore denticles. The outer ligament furrow is slitlike; I cannot distinguish a distinct ligament pit. There are traces of the transverse ridge, which quite evidently did not extend the full width of the plate. There are indications of fairly strong oblique fossae. The intermuscular notch is broad and the slopes of the muscle areas faced outward.

The radianal is a large plate which approximates anal X in size; the right tube plate is smaller. The proximal tip of the radianal extends to the suture between the posterior basal and the right posterior basal. On the left a sharp angle of the radianal limits, but does not cut off, the contact of anal X with the posterior basal below. On the right, the radianal extends to the tip of the right radial; distally the radianal bears the right tube plate. The right tube plate extends a short distance below the summit of the right posterior radial and its entire left side abuts against anal X. The left side of anal X contacts the left posterior radial. Details of the articular surfaces of anal X and the right tube plate are obscure, although the place of the outer ligament area in anal X is indicated

by traces of denticulations. I think it is quite likely that the articular surfaces of these two plates were in the same plane.

Two axillary primibrachs are preserved. These plates are wider than high, somewhat constricted at the sides, and lack keels. The articular surfaces for the secundibrachs resemble those of the radials, except that there is a definite ligament pit in the outer ligamentary area.

Discussion: In several respects this species resembles *Plummericrinus uddeni* (Moore and Plummer) although in *P. pittsburghensis* the interradianal notches are apparently less prominent, pits are present at the corners of plates, and there is a narrow contact between the posterior basal and anal X. In the holotype of *P. uddeni* the radianal is interposed between the posterior basal and anal X, consequently the latter two plates are not in contact. This arrangement of anal plates probably prompted Strimple (1961, p. 94) to refer *P. uddeni* to *Texacrinus*. However, as I have pointed out previously (p. 13) some species of *Plummericrinus* show this plate arrangement as a variation, and it may be anticipated that the same variation will be found in *P. pittsburghensis* when additional specimens are available.

Linear measurements, in millimeters, of the holotype specimen are summarized below. Because the specimen has been subject to compaction, length, rather than height measurements of the plates were taken.

Greatest width of cup	15.0*
Width of basal concavity	3.0
Width of infrabasal circlet	3.9
Length of basal (raB)	4.5
Width of basal (raB)	4.8
Length of radial (aR)	3.7
Width of radial (aR)	6.2
Length of suture between basals	2.8
Length of suture between radials	2.1
Length of radianal	3.9
Width of radianal	3.7
Length of anal X	3.5
Width of anal X	4.0
Length of right tube plate	2.6
Width of right tube plate	2.9
Length of first primibrach (C ray)	4.1
Width of first primibrach (C ray)	4.9

* Estimated

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THE HOBSON SITE: A FORT ANCIENT COMPONENT NEAR MIDDLEPORT, MEIGS COUNTY, OHIO

James L. Murphy

ABSTRACT

Salvage archeology at the Hobson Site (33Ms-2) on the Ohio River 1½ miles downstream from Middleport, Meigs County, Ohio, has revealed an important Fort Ancient component. On the basis of the dominant pottery types, the component is assigned to the Feurt Phase. It is suggested that the site represents the early Feurt Phase, and the age of the site is estimated as approximately 1100-1200 A.D. Minor traces of Archaic, Woodland, and later Late Prehistoric components were also noted.

INTRODUCTION

The Hobson Site (33Ms-2) located on the west bank of the Ohio River, 1½ miles downstream from Middleport, Meigs County, Ohio, was partly and hurriedly excavated in August, 1966. Mr. George Orahod of Prospect, Ohio, the construction engineer at the site, notified the author on the day that ground was broken. The following three days were spent by the author and another Ohio University student, Mr. Tim Watkins, in salvaging as much material as possible. The site is now the location of the new Middleport sewage treatment plant. It is regrettable that, although the plant had been in the planning stage for over ten years, we did not learn of the existence of the archeological site until after construction had started. On the other hand, it is fortunate that Mr. Orahod was interested in the site and notified both the Ohio Historical Society and Ohio University. In addition to Mr. Orahod, acknowledgment should be made to Mr. Emmett Conway of the Institute for Regional Development, Athens, Ohio, Mr. Ross Goodwin and Mr. Watkins, who were of help in the salvage operation, and to Mr. Conway, who photographed the burial found at the site.



LOCATION AND SITE DESCRIPTION

The site lies on the northern bank of Storys Run at the confluence of that stream with the Ohio River, $1\frac{1}{2}$ miles downstream from Middleport, Ohio, and $1\frac{1}{4}$ miles upstream from Lakin, West Virginia, at an elevation of approximately 570 feet above sea level. The bluff on which the site is located lies about 25 feet above the present normal pool elevation of the Ohio River. The land is now owned by the city of Middleport, and the site name is taken from Hobson Junction, slightly less than half a mile upstream, on the Chesapeake and Ohio Railroad.

Concentrated occupation occurred over an area of at least two acres, the heaviest midden occurring near the edge of the river bluff. Midden material averaged less than a foot in thickness, thinning rapidly to the north and east until, on the periphery of the site, only a few flint chips, potsherds, bone fragments, and clam shells were seen, the latter being the most conspicuous in the freshly exposed cuts made by the earth-moving equipment. Some areas of fire-burned subsoil were found near the river bank and clam shells were so abundant in the same area as to constitute a veritable shell midden. The only other features encountered were the dozen or so burials in the cemetery located at the northeast edge of the midden area.

Excavation technique, if it can be called that, consisted largely of surface collecting behind the earth-moving equipment as the machinery passed back and forth over the site. When the equipment was not in operation, portions of the midden were scraped down to the subsoil with mattocks. It was in this manner that the one complete burial excavated was first found, although it was removed with more care than we were able to give to excavation of the rest of the site.

FLINT AND STONE MATERIAL

Pl. 1

Relatively little chippage was recovered from the site, partly because in our haste it was thought preferable to concentrate on the bone, shell, and pottery refuse material. Of the 274 chips saved, 96 percent represented pebble chert collected from the river gravel. The bulk of this river chert is composed of Devonian and Pennsylvanian material, at least a third of it being dense black flint from

the Upper Mercer and Kanawha members. With the exception of a few chips of Flint Ridge (Vanport) flint, none of the remaining chippage could be identified.

Flint artifacts from the site include 13 triangular points of pebble chert which fall into three relatively distinct types: large, crude, possibly unfinished points (5), small, thin, well-made points with convex bases and concave sides (7), and small, thin points with straight sides and a straight base (1). Though admittedly a small sample, the predominance of the convex base in association with concave sides which frequently are produced to form basal ears may prove to be a temporally distinct point type. It is a distinct minority type on Feurt Phase Fort Ancient components in the Hocking Valley.

There are also three large blanks of river pebble chert, two broken elongate points (one of Brush Creek chert and the other of Kanawha flint), a broken, stemmed Adena point of an unidentified flint, and a side-notched Archaic point of Flint Ridge flint. The base of this last point is either fractured or else represents the original surface of the striking platform; the lower portions of the notches are moderately ground. A small, crude end-scraper on a blade, two long blade-like spalls with retouch flaking along a portion of one end, and four unidentifiable fragments of points complete the list of worked flint material.

The remaining stone artifacts consist of a small hematite celt and a roughly chipped basalt chopper. A single fragment of unworked cannel coal was also found.

WORKED BONE MATERIAL

Pl. 2

Bone artifacts were relatively uncommon at the site and consisted mainly of awls and bone beads. There are two bird-bone splinter awls, a deer-ulna awl, and the tip of a second deer-ulna awl. Bird bone was utilized for beads, two of which were recovered; there is also a fragmentary bead made from the radius of a rabbit. Other bone artifacts are a small piece of a turtleshell cup, part of a bone beamer, and a small, spatulate object apparently made from a deer longbone.

POTTERY

Pl. 3, 4

The potsherds collected at the Hobson Site may be divided into five distinct types based on differences in surface finish, temper, and rim decoration. Two of these types, however, are very poorly represented.

Type 1: Limestone-tempered, cordmarked ware represented by 25 body sherds and one rim sherd. Average thickness of ten body sherds ranging from 4.6 mm to 8.2 mm is 6.6 mm. Temper fragments measure up to 10 mm in diameter. The solitary rim sherd has a slightly everted, cordmarked lip with the cordmarking vertical on the rim area. Most of the sherds contain minor amounts of sand, presumably accidental inclusions in the paste.

This type, as represented in the collection, cannot be distinguished from the late Middle Woodland Watson Ware of the Upper Ohio Valley nor from the Late Woodland Peters Cordmarked Ware from the Scioto and Hocking Valley drainages.

Type 2: Shell-tempered, cordmarked ware represented by 30 body sherds and a single rim sherd. Average thickness of ten sherds ranging from 4.7 mm to 9.1 mm is 6.6 mm. The rim sherd is strongly everted, the rim forming an angle with the body of approximately 145°. Cordmarking is vertical at the rim, the lower half of which is decorated with crudely incised vertical lunules; the upper half of the rim has the cordmarking obliterated by horizontal brushing or combing. Insofar as is known, this decorated sherd is unique. There is certainly no reason to assign it to Fort Ancient, although the body sherds are indistinguishable from Fox Farm Cordmarked.

Type 3: Fox Farm Salt Pan: A single shell-tempered sherd apparently comes from a Fox Farm salt pan. Although the lip is missing, the curvature of the sherd makes such an assignment likely. Depth of the pan is estimated as having been about 4 cm.

Type 4: Shell-tempered, plain vessels with plain rims. This type is represented by 26 rim sherds which vary considerably in rim profile; 21 are nearly vertical with rounded (12), flattened (6), or incised (3) lips. Three sherds, possibly from the same vessel, have sharply everted, slightly thickened rims 1 to 2 cm wide. Two sherds have convex rims 35 to 40 mm wide, separated from the body of the vessel by a rather abrupt flexure. Although those sherds with sharply everted rims are indistinguishable from Madisonville

Plain rim sherds, the affinities of the bulk of the plain rim sherds lie with Griffin's Feurt Focus.

Type 5: Decorated rims which are considered to be variants of the plain shell-tempered ware (Type 4). The 791 plain, shell-tempered body sherds from the site cannot, of course, be separated into the two rim types. Among the decorated rims there are seven small sherds with multilinear incising and four small sherds with cord-wrapped stick impressed punctates, sherds too small for one to form an idea of the entire pattern. Sixteen sherds represent vessels which had horizontal multiple incising around the rim; the incised lines vary from four to six in number and from 1.9 mm to 3.3 mm in width. The incised lines vary from closely spaced (2.5 mm apart) to 15 mm apart. The incising is generally crude and the lines are only roughly parallel. In four instances there is an additional incised design element below the horizontal banding: alternating triangles filled with oblique incised lines, a crude, fine-lined rectilinear guilloche, and two sherds on which the incised pattern cannot be determined. Three rim sherds have the opposed chevron design considered typical of the Feurt Phase (Murphy, *ms.*).

A single sherd combines cord-wrapped stick punctates as a rim border and a rim decorated with oblique incised lines. The only other known occurrence of this motif is a sherd of Chillicothe Brushed from the McGraw Site (Prufer, *et al.*, 1965, p. 55), though it would be rash to postulate any direct relationship between the two sites.

Finally, there are ten strap handles or fragments of handles and two lug handles. One of the lugs is a mammiform lug detached from the vessel; the other is simply a small horizontal shelf or ridge attached to the lip. The strap handles are crudely made, large, with parallel sides. Two are punctate and have a castellated lip. One of these has a row of punctates at the base of the rim, as is the case with a third handle, which does not have castellations. Another strap handle occurs with a similar raised rim area rather than castellations, but it does not have punctates at the base of the rim. The remaining handles are fragmentary or detached from the vessels. Included in the count are two broken castellations which do not belong to any of the rims collected.

POTTERY SUMMARY

The strap handles recovered from the site certainly do not resemble Madisonville or "Clover Complex" material. Nor does the material strongly resemble Monongahela wares. It seems to fit best the known characteristics of the type Feurt Plain. The large amount of incised rim sherds would also suggest a relationship with the Feurt Phase, especially when one considers the prevalence of the opposed-chevron motif. The dominance at the site of smooth-surfaced shell-tempered sherds is an even more striking similarity between the Hobson Site and Feurt Phase components in the Hocking Valley.

At variance with our present knowledge of Feurt ware is the common use of horizontal incised motives at the Hobson Site. Such sherds are indistinguishable from sherds labelled Monongahela Incised from the Speidel Site, Ohio County, West Virginia (Mayer-Oakes, 1954, fig. 13, 14). However, it is interesting to note that Griffin (1943, pl. xx, fig. 1) illustrates an "atypical" Baum sherd with horizontal incising from the Feurt Site. A horizontal rim motif is also known from the McCune Site, Athens, Ohio, a Feurt component (Murphy, *ms.*). Even more significant is the dominance of horizontal incising at the Blain Site, a Baum-like component currently under study by Dr. Olaf Prufer, and its presence on shell-tempered ware from Cole Complex sites excavated by R. S. Baby.

It is tempting to suggest that horizontal incising is a carry-over from the Baum Phase into the early Feurt Phase, but such an hypothesis would certainly be premature. Unfortunately, because of the hurried manner in which the Hobson Site was excavated, it is a moot point whether one or two Late Prehistoric components are represented and, if two, whether or not they are contemporaneous. Until a definite Feurt site is discovered at which horizontal incising is a common decorative element, the best course to follow is to assign tentatively the incised Hobson sherds to Feurt Incised.

HISTORIC MATERIAL

Pl. 2

Numerous fragments of glass and china were noted at the site, although unfortunately none of the china ware was saved. The only recognizable metal objects found were a penknife and an unidentifiable fragment of cast iron. The foundations of an old farm-

house lay immediately to the northeast of the site, and the historic items may best be ascribed to that source.

The presence of an historic Delaware village site in this immediate area should be noted, although it is not thought to have been located at the Hobson Site. Lewis Evans' 1755 map locates "Kishkeminetas old T." on the north side of the Ohio River, slightly less than half way between "The big Bent" and the Kanawha River. Hanna (1911, v. 2, p. 142) locates Kiskiminetas' Town eight miles above the mouth of the Kanawha, which would place it in the vicinity of the town of Cheshire, 2½ miles downstream from the Hobson Site. The limited time available did not permit a general survey of the area, but it is believed that such a survey would discover the exact location of Kiskiminetas' Old Town.

BURIALS

Pl. 5, 6

The cemetery associated with this village site lay immediately to the northeast of the midden deposit, possibly extending even as far as the farmhouse mentioned above. At least nine burials were noted, scattered over an area of about an acre, between the major area of occupation and the foundations of the farm house. The burials were uncovered by large earth-moving equipment which removed them completely within the course of an hour. Already badly damaged by the first swath cut by the excavating equipment, none of the burials were salvaged. No grave goods were noted, and all of the burials appeared to be flexed or semi-flexed.

The single burial retrieved from the Hobson Site was discovered in the midden area, about ten yards from the river bank. It lay from 6 to 12 inches below the surface but did not extend into the yellow subsoil; there was no noticeable grave outline. The burial was semiflexed, with legs folded, right arm at the side, and left forearm placed on the abdomen. The patellae, distal ends of the femora, and proximal ends of the tibiae had been removed by plowing, but the rest of the burial was in good condition. Although no grave goods accompanied the burial, the individual is unusual in showing abundant evidence that he had been either murdered or executed. The first and third lumbar vertebrae contain triangular projectile points which are lodged in the ventral portion of the centra and must therefore have penetrated the abdomen. Two addi-

tional flint projectile points were found, one in the chest cavity and the other touching the medial edge of the right scapula. Finally, there was an antler projectile point located in the chest cavity.

Skeletal measurements are presented in table 1. It should be noted that the skull was somewhat distorted by warping, so that some of the measurements are only approximate at best. The individual was male and, based on the dentition and features of the pubic symphysis, 22 to 23 years of age. Dental caries had begun to develop only on the upper right second molar, the upper first molars, and the lower molars; even here decay was confined to small "pin-hole" perforations, the largest measuring .9 mm in diameter. The mandibular molar cusp pattern is of the Y-5 type only on the first molar; that of the second is of the +5 type. Excessive crowding of the incisors and canines had produced moderate malocclusion. The presence of Wormian bones may also be noted, as well as the presence of an olecranon perforation in the left humerus. A very interesting pathological condition of the skeleton is the ankylosis of a portion of the vertebral column, all nine vertebrae from the second cervical to the third thoracic being fused. When compared with the skeletal data available from the Madisonville Site (Hooten, 1922, p. 83-134), three differences are noted: the basion-bregma length is greater than that found in nearly all of the Madisonville crania, the angle of the mandible is smaller than that of any of the Madisonville mandibles, and the nasal index is slightly lower than any of those given for the Madisonville skeletons. It is unfortunate that none of the other burials were recovered, but if the measurements of a single skeleton can be given any weight, it is likely that the inhabitants of the Hobson Site were physically distinct from the Madisonville people.

VERTEBRATE FAUNA

A list of the species identified in the bone refuse is given in table 2 and requires little comment. Butchering marks were noted on 29 deer bones: 7 astragali, 8 humeri, 4 ulnae, 2 scapulae, 2 radii, 5 calcanea, and 1 femur. The cuts on the humeri were more proximal than the similar marks described by Guilday *et al.* (1962, p. 73 fig. 8) from the Eschelman Site and were generally located on the shaft or the very base of the shaft. One of the right calcanea is unusual in having cut marks on the anteroproximal surface of the bone. The femur has two cut marks on the lateral surface of the

great trochanter. The wolf ulna has a sharp cut on the posterolateral surface of the olecranon, at the top of the semilunar notch.

Measurements of the 17 measured deer astragali, in millimeters, are as follows:

	Length	Width	Thickness
Mean	39.8	25.9	22.6
Range	35.4-42.6	24.5-27.8	21.0-24.1

These measurements are significantly lower than those from the Eschelman Site, but the explanation probably lies in there being a greater proportion of does and young animals at the site rather than the presence of a subspecies characterized by its small size. The 12 deer jaws that could be age-graded form a uniform series ranging from about 8 months to 6 years of age, seven of the specimens falling within the 3 to 4 year age bracket.

NAIAD MATERIAL

As mentioned in the description of the site, freshwater clam shells were so abundant in portions of the site that the term shell midden was applicable to those areas. The list of species is given in table 3. Noteworthy is the presence of *Quadrula metanevra* var. *wardi*, considered a small river and creek form, which might suggest that the shellfish were collected from both the Ohio River and its tributary, Storys Run. Ortmann (1919, p. 49-50), however, notes occurrences of this form as far down the Ohio River as Parkersburg. The present occurrence would merely extend the distribution slightly farther downstream. Comparison with faunal lists from the Childers, Globe Hill, and East Steubenville sites, 150 miles upstream, reveals relatively few differences. The complete absence of *Cyclonaias* and *Ptychobranhus* in such a relatively large sample is difficult to explain, but the only other differences are a comparatively greater percentage of *Elliptio crassidens* and *Quadrula cylindrica* at the Hobson Site.

CONCLUSIONS

The Hobson Site has yielded slight evidence of occupation during Archaic, Late Woodland, and late Late Prehistoric times. The major occupation occurred during middle Late Prehistoric times, during the Feurt Phase, and probably rather early in that phase. The only Feurt component having yielded an acceptable radio-

carbon date is the McCune Site at Athens, Ohio (Murphy, *ms.*) which yielded a date of 1235 A.D. The 1180 A.D. date for the Graham Site, a Baum component at Logan, Hocking County, Ohio, would seemingly pinpoint the date of the Hobson Site as very close to 1200 A.D. If importance is attached to the similarity between the Hobson ware and as yet undescribed pottery from the Blain Site, the date might be estimated as closer to 1100 A.D., for the Blain Site itself dates around 1000 A.D. (O. H. Prufer, personal communication, June, 1967). Affinities can also be seen with the Speidel Site, which has been referred to the Monongahela Complex. Although apparently close to the historic Kiskiminetas Town, it is unlikely that the Hobson Site is the exact location of that settlement.

It is regrettable that the Hobson Site could not have been excavated with the care and thoroughness it deserved. The material salvaged from the construction site provides a glimpse of what might be expected from a site transitional from the Baum to the Feurt Phase. Griffin (1943, p. 209) speaks of the region between the Madisonville and Feurt sites as "terra incognita," and the same might be said for that portion along the Ohio River between Proctorville and Marietta. If the Hobson Site is typical, this region must contain numerous rich and important sites as yet untouched though rapidly being destroyed.

TABLE 1
SKELETAL MEASUREMENTS AND INDICES
(Measurements in millimeters)

Cranial Measurements

a Glabello-occipital length	183	l Nasal breadth	24
b Maximum breadth	136	m Orbital height—left	37
c Basion-bregma height	147	n Orbital breadth—left	41
d Mean thickness left parietal	4.4	r Interorbital breadth	18
e Minimum frontal diameter	91	s Biorbital breadth	101
c' Auricular height	121	t External palate length	54
Horizontal circumference	507	u External palate width	67
Nasion-opisthion arc	355	v Condyllo-symphyseal length	105
Transverse arc	323	w Bicondylar width	128
f Bizygomatic diameter	124	x Height of symphysis	38
(Midfacial breadth)			
g Total facial height	128	mh Mandibular height	58
h Nasion-prosthion height	73	y Bigonial diameter	110
i Basion-nasion length	110	Minimum breadth of left	
j Basion-prosthion length	96	ascending ramus	37
k Nasal height	55	Mean angle of mandible	113°

Cranial Indices

b/a Cranial index	74.2	y/e Fronto-gonial index	121
c/a Length/height	80.3	e/f Zygo-frontal index	73
c/b Breadth/height	108	m/n Left orbital index	90.2
$\frac{a+b+c}{3}$ Cranial module	155.3	r/s Interorbital index	17.8
e/b Fronto-parietal index	66.9	l/k Nasal index	43.6
g/f Total facial index	81.8	u/t External palatal index	125
h/f Upper facial index	50	v/w Mandibular index (1)	82
f/b Cranio-facial index	91.2	mh/v Mandibular index (2)	55.2
y/f Zygo-gonial index	81.5		

Postcranial Measurements

	Left	Right	Femur (cont.)	Left	Right
Humerus	320	340	Middle anteropost.		
Maximum length			diam.	27.5	26.2
Maximum diameter of head	---	48	Middle lateral diam.	25.7	25.7
Maximum middle diameter	21.3	21.8	Middle circum.	86	87
Minimum middle diameter	15.1	15.5	Tibia		
Middle circum.	62	64	Maximum length	---	360
Ulna			Nutrient foramen anteropost. diam.	40	39
Maximum length	---	266	Nutrient foramen lateral diam.	22.7	21
Middle circum.	43	41	Middle anteropost. diam.	34	35.2
Radius			Middle lateral diam.	19.9	20.2
Maximum length	251	---	Middle circum.	87	90
Middle circum.	36	37	Clavicle		
Femur			Maximum length	153	149
Maximum length	---	---	Middle circum.	31	30
Maximum diameter of head	44.3	45.7	Innominate		
Subtrochanter anteropost. diam.	31.6	34.4	Height	---	212
Subtrochanter lat. diam.	25.8	26.4	Breadth	147	146

Postcranial Indices

Humerus			Fibula		
Middle index	70.9	71.1	Robustness index	12.4	---
Robustness index	19.4	19.2	Tibia		
Ulna			Platycnemic index	56.8	53.8
Robustness index	---	15.5	Middle index	58.9	57.4
Radius			Robustness index	---	25
Robustness index	14.3	---	Clavicle		
Femur			Robustness index	20	20
Platymetric index	78.8	76.7	Innominate		
Middle index	93.4	98.1	Innominate index	---	68.9

TABLE 2
VERTEBRATE REMAINS FROM THE HOBSON SITE

Species	No. of bones	Percentage
Fishes:		
Catastomid sp.	2	
<i>Aplodinotus grunniens</i> Rafinesque	1	
<i>Ictalurus</i> sp.	3	
Unidentified	9	
Reptiles:		
<i>Terrapene carolina</i> (Linnaeus)	27	4.3
<i>Chelydra serpentina</i> Linnaeus	6	
Birds:		
<i>Meleagris gallopavo</i> Linnaeus	95	15.3
Unidentified	11	
Mammals:		
<i>Odocoileus virginianus</i> (Zimmermann)	429	69.0
<i>Procyon lotor</i> (Linnaeus)	18	2.9
<i>Sciurus</i> sp.	9	1.4
<i>Cervus canadensis</i> Erxleben	9	1.4
<i>Castor canadensis</i> Kuhl	4	
<i>Tamias striatus</i> (Linnaeus)	3	
<i>Sylvilagus floridanus</i> (Allen)	2	
<i>Ursus americanus</i> Pallas	2	
<i>Canis lupus</i> Linnaeus	1	
Unidentified large mammal bones (probably deer)	122	
Unidentified mammal bones	408	
Total number of identified bones	611	

TABLE 3
MOLLUSCAN REMAINS FROM THE HOBSON SITE

Species	Minimum No.*	Percentage
Pelecypoda:		
<i>Amblema plicata</i> (Say)	10	5.0
<i>Quadrula cylindrica</i> (Say)	18	9.0
<i>Q. metanevra wardi</i> (Lea)	9	4.5
<i>Q. pustulosa</i> (Lea)	2	
<i>Pleurobema cordatum</i> (Rafinesque)	69	34.5
<i>P. pyramidatum</i> (Lea)	3	
<i>P. clava</i> (Lamarck)	7	3.5
<i>Elliptio dilatatus</i> (Rafinesque)	3	
<i>E. crassidens</i> (Lamarck)	67	33.5
<i>Obovaria subrotunda</i> (Rafinesque)	2	
<i>Proptera alata</i> (Say)	1	
<i>Ligumia recta latissima</i> (Rafinesque)	3	
<i>Lampsilis ovata</i> (Say)	5	
<i>L. siliquioidea</i> (Barnes)	1	
	200	

* The minimum number of individuals, based upon the maximum number of either left or right valves of each species.

Gastropoda:

<i>Anguispira alternata</i> (Say)	45
<i>A. kochi</i> (Pfeiffer)	21
<i>Mesodon clausus</i> (Say)	7
<i>Triodopsis tridentata</i> (Say)	1
	<hr/>
	74

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EXPLANATION OF PLATES

Plate

1. Stone and flint artifacts. Bottom row: Triangular points and two flake knives. Second row: Triangular points. Third row: Side-notched, stemmed, and corner-notched points; two triangular blanks. Top row: Small hematite celt, two large flint scrapers or choppers, and a crude triangular point.
2. Bone artifacts and historic material. Bottom row: Penknife and unidentifiable fragment of cast iron; bird bone bead. Top row: Deer ulna awl, bird bone bead, spatulate bone object, antler point, and two bird bone awls.
3. Pottery. Bottom row: Incised and plain lips on rim sherds of Feurt Plain. Note absence of flare on both sherds. Second row: Castellated, punctate strap handle (Feurt) and everted rim sherd (Madisonville?). Top row: Two Feurt strap handles, both with punctate borders, one with punctate handle and castellations, the other with plain handle and raised rim area.
4. Pottery. Bottom row: Unusual incised sherd with basal punctations (photographed obliquely to show decoration), punctate and cordmarked body sherds. Middle row: Horizontal and diagonally incised sherds, Feurt Incised (?). Top row: Watson Ware limestone-tempered, cordmarked rim; plain convex, shell-tempered rim, and unique shell-tempered, cordmarked rim with brushed and incised motif.
5. Single excavated burial: arrows show two associated triangular flint points and location of two other associated points.
6. Four lumbar and one thoracic vertebrae with imbedded triangular flint points.



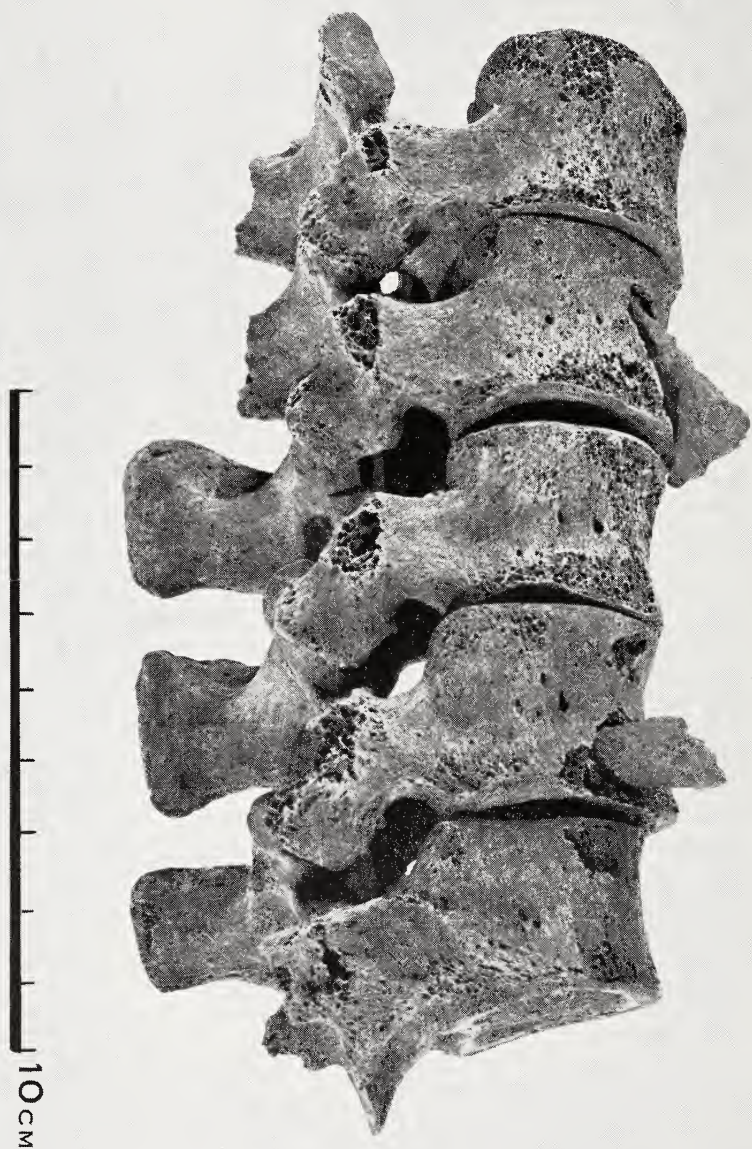


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AN ANTIACODONT FROM THE GREEN RIVER EOCENE OF UTAH

J. J. Burke

ABSTRACT

Report is made of a new occurrence of the dichobunid artiodactyl genus *Antiacodon* following its discovery in the Green River Formation in northeastern Utah by a Cleveland Museum of Natural History field party in 1967. A right ramus of the lower jaw with P_4 , M_{1-3} is described and identified as *Antiacodon pygmaeus* (Cope).

In August, 1967, a field party from the Cleveland Museum of Natural History made a search for vertebrate fossils in various Eocene formations of the Uinta Basin, Utah. During a brief visit to the Powder Wash collecting site in the Green River Formation in Uintah County, Utah, near the Utah-Colorado state line, Mr. William Hlavin of the Museum party found part of a lower jaw of the dichobunid artiodactyl *Antiacodon*, hitherto unreported from the Utah Green River beds.

The specimen is described in the present paper. Originally a more extensive study of *Antiacodon* was projected and was already under way before I learned that Carnegie Museum also has some *Antiacodon* material from the Powder Wash locality. Dr. Craig Black of that institution is presently engaged in a study of various Eocene artiodactyles of this type. Inasmuch as there is no point to my duplicating Dr. Black's work, I am limiting the present paper to description of the specimen at hand.

The illustrations accompanying this paper are from superb pencil drawings of the specimen prepared by Mr. Lawrence B. Isham.

SYSTEMATIC PALEONTOLOGY

Family DICHOBUNIDAE Gill, 1872

Subfamily ANTIACODONTINAE Gazin, 1958

Genus ANTIACODON Marsh, 1872

ANTIACODON PYGMAEUS (Cope), 1872

Fig. 1

The specimen, C.M.N.H. no. 10930, consists of most of the right ramus of the mandible with P_4 , M_{1-3} . It was contained in a block of sandstone taken from the Powder Wash locality, designated by Dawson (1968) as "two miles southeast of Powder Springs (sec. 8,

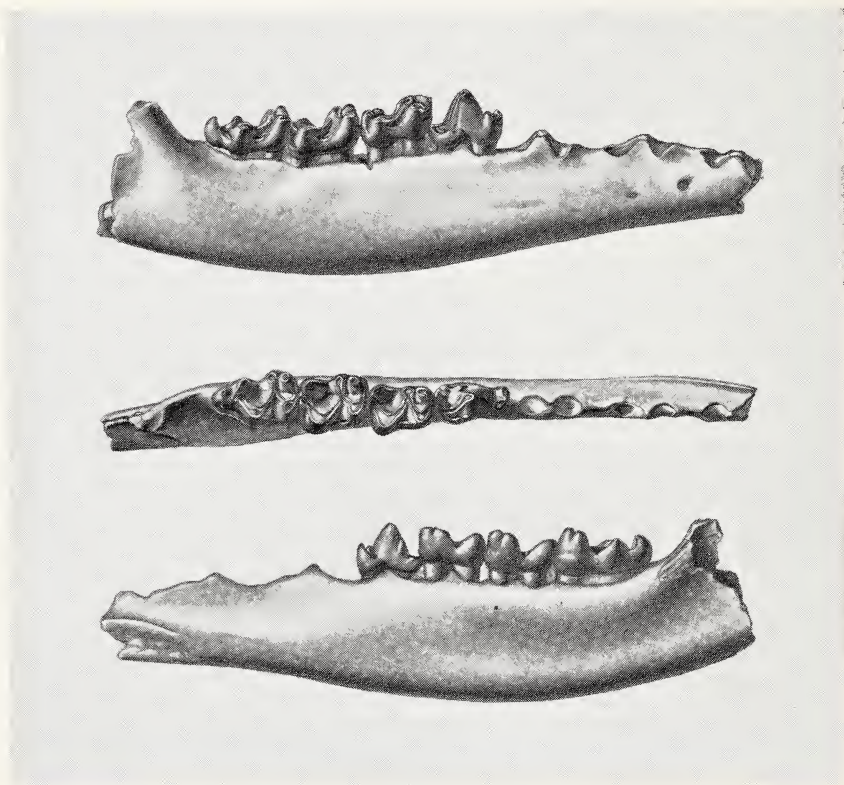


Fig. 1

Antiacodon pygmaeus (Cope). Right ramus of mandible (C.M.N.H. no. 10930), lateral, occlusal and lingual views. Twice natural size. Douglas Creek Member, Green River Formation, Middle Eocene, Powder Wash quarry, Uinta Basin, Utah.

T. 7 S., R 25 E., S.L.M.), Uintah County, Utah, on the basin side of Raven Ridge in the eastern part of the Uinta Basin." Dawson also states that the United States Geological Survey has determined that the mammal quarry is in the lower part (Douglas Creek Member) of the Green River Formation. Although I indicated the assignment with question (Burke, 1935), my attributing the sandstone of the mammal quarry to the upper part of the Green River Formation remains a regrettable error.

Posteriorly, the lower jaw preserves part of the ascending ramus and the anterior portion of the masseteric fossa. Anteriorly it extends slightly in advance of the anterior border of the alveolus of the canine. About 2 mm of the ventral border is missing beneath M_1 ; the thin enamel walls of the hypoconids of M_2 and M_3 have been chipped, and most of the entoconid cusp of M_1 has been lost. All of these features have been restored in the illustrations (fig. 1).

The masseteric fossa is fairly well excavated, although its inferior border is not well defined. The anterior border of the ascending ramus rises at an angle of about 65 degrees. The ventral border of the ramus is slightly convex, and the anterior half curves gently upward. There are three mental foramina, a slight slitlike one beneath the posterior alveolus of P_3 , another beneath the posterior alveolus of P_2 , and the third and most prominent beneath the diastema between P_1 and P_2 .

The alveoli for the premolars anterior to P_4 indicate two diastemata, one between P_2 and P_3 and a second, slightly shorter, between P_1 and P_2 . The single alveolus for P_1 is separated from the alveolus for the canine by about 1 mm of bone and the root of P_1 appears to have been slightly larger than that of the canine.

The anterior portion of the ramus is slender because of the upcurving of the ventral border and the progressive downbending of the alveolar border. The symphysis is extensive and quite rough; it narrows posteriorly, and extends back beneath the alveoli for P_2 .

The protoconid of P_4 is a strong cusp, attenuated anteriorly to meet with a prominent paraconid. Internal to, and extending in advance of the paraconid is a relatively large parastylid. The metaconid, which arises on the posterointernal flank of the protoconid, is a distinct cusp, but definitely smaller than is usual in *Antiacodon*. The talonid is defined by the cingulum externally

and is joined posteriorly by the strong posterior crest from the protoconid. On the internal side of the talonid there is a small but definite entoconid, from which a short crest extends to the metaconid.

All of the molars bear anterior and posterior cingula, although the anterior cingulum of M_3 is barely distinguishable. Low cingula also block the exits of the external valleys of the molars.

The trigonids of the molars are characteristic of *Antiacodon*. The metaconids and paraconids are closely appressed, with the paraconid the higher and larger cusp. The metaconid extends further lingually than the paraconid. The protoconid is the lowest trigonid cusp and might be termed subcrescentic. An anterior crest from the protoconid joins the paraconid. A less elevated crest extends from the protoconid to the metaconid.

The molar talonids show large crescentic hypoconids and broad central valleys, the exits of which are closed by the metaconid and the entoconid walls, which form a broad V and meet low on the lingual side. The valley slopes of the entoconids are decidedly flat surfaces. From the hypoconid the crista obliqua extends to the protoconid-metaconid crest in M_2 and M_3 ; in M_1 the crista obliqua extends well up on the slope of the metaconid. The posterior crest from the hypoconid connects with the hypoconulid, but not with the entoconid, in M_1 and M_2 . In M_3 this crest connects with the posterior blade of the entoconid. The crestlike entoconid blade then descends poster^{ex}o-internally toward the base of the hypoconulid. The posterior cingulum originates along the posterior walls of the hypoconid and entoconid and expands posteriorly to form the prominent hypoconulid. An incipient crest extends forward and downward along the anterior face of the hypoconulid to meet with the descending blade of the entoconid. The posterior crest from the hypoconid very definitely does not extend to the hypoconulid.

Discussion: Gazin (1952, 1955, 1958, 1962) has dealt rather extensively with *Antiacodon* in relation to other Eocene artiodactyl genera. Based on his studies, I think there can be little doubt that the present specimen represents *Antiacodon pygmaeus* (Cope).

Although the small metaconid of P_4 of C.M.N.H. no. 10930 is not typical of *Antiacodon pygmaeus*, it appears to me that this may be simply a matter of individual variation, and Dr. Gazin, who has

had an opportunity to see the specimen, accords with me in this conclusion (written communication, Feb. 1, 1968).

Also to be considered are variations in the length of diastemata in specimens that have been referred to *Antiacodon pygmaeus*. Gazin (1958, p. 3) has noted that the diastema between P_2 and P_3 in A.M.N.H. no. 12697 is about 2.5 mm and in U.S.N.M. no. 1800 it is 3.9 mm. He also states (ibid., p. 4) that the jaw of A.M.N.H. no. 12697 is preserved to about 1.7 mm in advance of the roots of P_2 , but doubtless he found no trace of an alveolus, otherwise he would have noted it. The diastema between P_2 and P_3 in C.M.N.H. no. 10930 is 1.9 mm, definitely shorter than in either of the above specimens, and the diastema between P_1 and P_2 is 1.7 mm, so this diastema also is apparently shorter than in A.M.N.H. no. 12697. However, I am inclined to attach little weight to these variations; they may, as a matter of fact, be related to age—the teeth of U.S.N.M. no. 1800, for example, are considerably worn in comparison with those of C.M.N.H. no. 10930, and my specimen quite obviously represents a much younger individual.

Because C.M.N.H. no. 10930 preserves more of the anterior portion of the jaw than previously described specimens of *Antiacodon*, it is of particular interest. It demonstrates, for instance, that by Middle Eocene time the P_1 of *Antiacodon* had attained the same size as the canine or was perhaps a little larger. But it also shows that along with the enlarged P_1 the anterior portion of the jaw remained, as Gazin (1958, p. 4) characterized it, “relatively slender” and the downbending of the alveolar border anteriorly contributes to this slenderness to about the same extent as the upcurving of the inferior border.

Starting with these characteristics, I would expect an Upper Eocene descendant of *Antiacodon* to show much the same construction of the lower jaw, and along with it no pronounced increase in size of P_1 —in effect, the type of jaw usually found in Upper Eocene homacodonts.

Gazin's (1958) *Auxontodon* combines a lower jaw with a strongly convex inferior border and a much enlarged, perhaps caniniform, P_1 . The cusp-crest construction of the cheek teeth appears to conform in all respects with what one would expect of an Upper Eocene antiacodont. Nevertheless, for the reasons cited

above, I cannot visualize *Auxontodon* as a direct derivative of *Antiacodon*, although there seems no doubt that the two forms had common ancestry.

Possibly, as has been suggested in regard to other elements of the North American Middle Eocene fauna, *Antiacodon* may have been in some way too specialized for a particular environment to survive its passing. Study of the skeleton might throw some light on the matter, but despite years of collecting, skeletal material of these Middle Eocene artiodactyles is still unknown. To judge from teeth at least, *Antiacodon pygmaeus* appears to be the only artiodactyl represented in the Powder Wash fauna. Almost any artiodactyl skeletal material taken from that quarry might prove to belong to *Antiacodon pygmaeus* and would be worthy of study on this account.

Measurements of C.M.N.H. no. 10930, in millimeters, are given below:

Depth of lower jaw at posterior margin of alveolus of P_1	5.0
Depth of lower jaw at anterior margin of first alveolus of P_3	6.0
Depth of lower jaw beneath M_2 , lingually	7.5
Length of cheek tooth series from anterior margin of alveolus of C to posterior margin of M_3	35.5
Length of cheek tooth series from anterior margin of alveolus of P_1 to posterior margin of M_3	33.9
Length of diastema between P_1 and P_2	1.7
Length of diastema between P_2 and P_3	1.9
Length of lower premolar series from anterior margin of alveolus for P_1 to posterior margin of P_4	18.9
Length of lower molar series, M_1 - M_3 inclusive	15.0
P_4 , length : greatest width	4.6 : 2.5
M_1 , length : greatest width	4.5 : 2.9*
M_2 , length : greatest width	4.4 : 3.4*
M_3 , length : greatest width	5.8 : 3.3

*Approximate

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MANUSCRIPT RECEIVED DEC. 5, 1968

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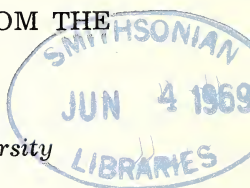
MARCH 14, 1969

NUMBER 6

A TEMNOSPONDYLOUS LABYRINTHODONT FROM THE LOWER CARBONIFEROUS

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ABSTRACT

An amphibian skull and partial skeleton from the basal part of the Mauch Chunk Group of the Mississippian of West Virginia is that of a colosteid temnospondyl described as *Greererpeton burkemorani* gen. et sp. nov.

INTRODUCTION

Although amphibian remains are plentiful in the late Carboniferous (the Pennsylvanian Period of American terminology), they are exceedingly rare in the earlier Carboniferous (the Mississippian). In this paper there is described for the first time a labyrinthodont amphibian skull from the Mississippian of North America. Until recent decades Lower Carboniferous amphibian remains were absolutely unknown except in Scotland, and even there specimens were few. All materials of that age then available were described by Watson in 1929. Once there are excluded certain specimens now known to be Upper rather than Lower Carboniferous in age (Panchen and Walker, 1961), the list of finds is a meager one. There are a few lepospondyls, mainly "adelospondyls" of Watson's terminology; of labyrinthodonts, one skeleton (*Pholidogaster*); seven skulls, most of the peculiar loxommid type, with keyhole-shaped orbits; a few fragmentary remains.

In North America, no Mississippian amphibians were known until relatively recently. In 1941, I reported the discovery of remains of amphibians in the Hinton Formation of the Mauch Chunk Group in West Virginia; the bones present, however, were disarticulated and generally fragmentary, and hence of little mor-

phological or evolutionary value. In 1955 I decided to initiate a new series of attempts to find sites and materials of American Carboniferous amphibians. Considerable Pennsylvanian material was found, but the only earlier find of value was that of a jaw of very late Mississippian age, apparently of an anthracosaur, in the Point Edwards Formation of the Canso Group in Nova Scotia (Romer, 1958). Further exploration for Carboniferous amphibians has been continued with success by Dr. Baird of Princeton and Dr. Carroll of McGill, principally in Nova Scotia. Again, however, their finds have been mostly Pennsylvanian, and the only Mississippian specimen reported is a partial skull of the loxommid from the Point Edwards Formation (Baird, 1962).

Of especial interest for some time, in the Lower Carboniferous of the Allegheny region, has been a quarry at Greer, West Virginia. On several occasions this was visited by parties from the Museum of Comparative Zoology; amphibian material was found, but of a fragmentary nature. More successful have been Mr. John J. Burke and Mr. William E. Moran who had earlier searched intensively in the "tri-state area" of West Virginia-Pennsylvania-Ohio for Carboniferous and early Permian vertebrates (Moran, 1952; Romer, 1952). Materials collected by them at Greer, including a skeleton which is apparently anthracosaurian, are in the U. S. National Museum collections. The present specimen from Greer not only forms an addition to our sparse representation of Lower Carboniferous labyrinthodonts, but also is important because it increases our knowledge of the stratigraphic distribution of labyrinthodont types.

In his classic papers of 1919 and 1926, Watson, for the first time, sorted out the then chaotic array of labyrinthodonts into a reasoned series of subgroups. The Triassic members, he pointed out, form the Stereospondyli, with intercentra enlarged and pleurocentra generally absent. These are clearly derivable from the Rhachitomi, abundant in the Permian, in which in each segment there were paired small pleurocentra and a fairly large intercentrum. The only type of Carboniferous vertebrae known to Watson were of the embolomere type, in which both intercentrum and pleurocentra form complete rings. He therefore concluded that the embolomeres were the ancestral labyrinthodonts, and that the evolutionary sequence ran: embolomeres — rhachitomes — stereospondyls.

This, when Watson proposed it, seemed a reasonable arrangement. But with the passage of time and augmented knowledge of fossil labyrinthodonts, the Watson classification became increasingly

unsatisfactory. Therefore, I proposed (Romer, 1947) a different phylogenetic scheme, with the labyrinthodonts arrayed dichotomously in two major subdivisions, Temnospondyli and Anthracosauria. Since vertebrae similar to the rhachitinous type are found among the ancestral crossopterygians, I suggested that this was the basic vertebral structure among labyrinthodonts, and that a main central group of these forms, to be termed Temnospondyli, continued on as Rhachitomi through the Carboniferous and Permian, to terminate in the Stereospondyli of the Triassic. A major side branch, to be termed the Anthracosauria, consisted of forms in which, in contrast to temnospondyls, the small paired pleurocentra of ancestral types became enlarged and fused to form a solid ring-shaped centrum. Here the major evolutionary line led, with eventual reduction of the intercentrum, to the Reptilia, with the Seymouriamorpha as a morphologically transitional group; the Embolomeri, instead of being truly primitive forms, appear to be an anthracosaurian side branch in which the intercentrum forms a complete ring, as do the pleurocentra.

When my scheme of labyrinthodont classification was first proposed, its base in actually known materials was none too secure, mainly because of the dearth of pre-Pennsylvanian finds. However, over the last two decades new studies and new finds have tended increasingly to support it. The description of postcranial remains of the late Devonian ichthyostegids (Jarvik, 1952) strengthens the conclusion that the rhachitinous vertebral type is primitive among amphibians. Restudy of *Pholidogaster* from the Lower Carboniferous of Scotland (Romer, 1964) beautifully illustrates a stage demanded by theory in the development of the pleurocentra toward the "holospondylous" condition of advanced anthracosaurians.

There still remained, however, a major gap in the early history of the Temnospondyli. Rhachitomes, contrary to Watson's earlier beliefs, are now known (mainly through studies by Baird and Carroll) to have been abundant and varied in the Pennsylvanian, but were long thought to be absent in the early Carboniferous. At the time I proposed the phylogenetic scheme here followed, I suggested that the peculiar loxommids, present in the early as well as late Carboniferous, were rhachitinous rather than embolomeric, as Watson had believed. This has since been shown by Baird (1957) to be the case. But surely other rhachitomes in addition to the aberrant loxommids, with their peculiar keyhole-shaped orbits, must already have been present in the Mississippian. The present

find of a Mississippian rhachitome of more normal structure adds major support to the belief that the Rhachitomi were already flourishing in early Carboniferous times.

PROVENANCE OF THE SPECIMEN

The materials here described were collected from the quarry at Greer, Monongalia County, West Virginia, by Mr. Burke and Mr. Moran; this site is a commercial limestone quarry, located on Deckers Creek, about 6½ miles southeast of Morgantown. The quarry region has been described by Tilton (1928), Coryell and Sohn (1938) and McCue, Lucke and Woodward (1939). The material quarried is a massive limestone of the Greenbrier Group. Mr. Thomas Arkle, Jr. of the West Virginia Geological Survey states (written communication, Jan. 7, 1969) that this bed is identified as the Union Limestone, which at Greer Quarry is overlain by the Bluefield Formation of the Mauch Chunk Group. These determinations are in keeping with studies by Wells (1950) and Flowers (1956).

Mr. Burke informs me that the specimen is derived from the Bickett Shale of the Bluefield Formation. The base of the Bickett Shale is about 16 feet above the Union Limestone at the Greer Quarry. The specimen is probably from the lower two to three feet of the Bickett, but its exact horizon is uncertain, since the rock had fallen from the face of the quarry.

The specimen is, thus, older than the fragmentary remains from the Hinton district, derived from a horizon considerably higher in the Mauch Chunk, and still older than the Nova Scotia remains mentioned above. As noted by Weller and others (1948), correlation of Lower Carboniferous American formations and zones with those of Europe is as yet none too certain, but the Greenbrier and basal Mauch Chunk seem certainly to equate roughly with the upper part of the Viséan of European terminology, and are pre-Namurian. The oldest European Carboniferous labyrinthodonts are from the "Carboniferous Limestone", Namurian in age. (A few lepospondyls come from the earlier Oil Shale Group.) Specimens from the Greer locality thus appear to be the oldest labyrinthodonts yet known except for the East Greenland ichthyostegids.

The remains here described are in all probability those of a single individual. A principal block includes the skull and jaws with, close behind, a disarticulated series of vertebrae and ribs

together with belly scales which, because of the presence of elements of the shoulder girdle and front limbs, obviously represent the anterior part of the trunk. A second series of vertebrae, ribs, and scales found to the rear of the main block appear to represent the more posterior region of the trunk. Nearby were a few other finds of limb and girdle bones, ribs and scales. Since vertebrae and scales in all cases are of the same type and since the limb and girdle elements form a nearly complete set of appropriately matching size for a single individual, it is reasonable to conclude that we are dealing with the disarticulated remains of one animal. The specimen is entered as no. 10931 in the collection of the Cleveland Museum of Natural History.

I am greatly indebted to the authorities of the Cleveland Museum of Natural History for the privilege and pleasure of describing this specimen. I also wish to acknowledge help from Mr. Thomas Arkle, Jr. and the West Virginia Geological Survey for information concerning the stratigraphy of the Greer area.

SYSTEMATIC PALEONTOLOGY

Family COLOSTEIDAE Romer, 1930

Genus **GREERERPETON**¹ gen. nov.

GREERERPETON BURKEMORANI² sp. nov.

Figs. 1-7

Diagnosis for genus and species: A colosteid rhachitome, similar in skull roof pattern and proportions to *Colosteus*, but with a lesser development of the anterior portions of the lateral line groove system; premaxillary "tusks" present, as in *Erpetosaurus*.

Holotype: Cleveland Museum of Natural History no. 10931.

Occurrence: Bickett Shale of the Bluefield Formation, Mauch Chunk Group, Mississippian.

Locality: Greer, Monongalia County, West Virginia, on Deckers Creek, about 6½ miles southeast of Morgantown.

Repository: Cleveland Museum of Natural History.

¹ The generic name is derived from the locality.

² The specific name is formed (reasonably if unorthodoxly) by combining the surnames of the two discoverers of the specimen.



Fig. 1. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Photograph of the main block containing the skull and remains of the anterior part of the trunk, $\times \frac{2}{3}$.

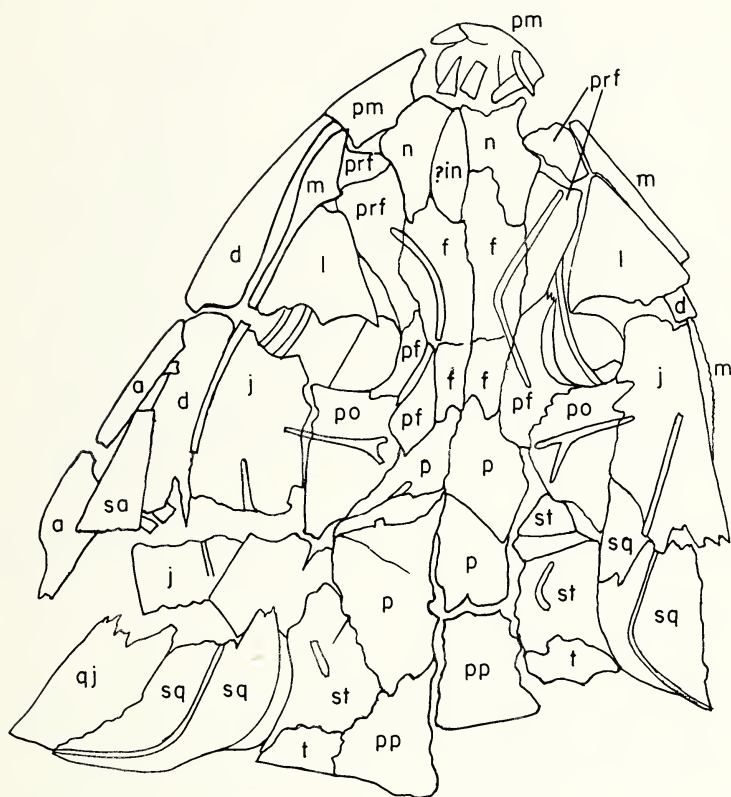


Fig. 2. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Key to elements present on the skull, as preserved: a, angular; d, dentary; f, frontal; ?in, internasal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; t, tabular, $\times \frac{2}{3}$.

DESCRIPTION

Cranial remains: The principal block (figs. 1 and 2) contains the entire cranial structure, with the skull, seen from above, crushed flat and somewhat disarticulated. Most of the left jaw ramus is seen to the left of the skull (the articular region and partial surangular were removed during preparation); the right ramus is mainly concealed by the skull, but the articular region is seen behind the right tabular. Except for the right quadratojugal and the anterior end of the left jugal, nearly the entire series of dorsal dermal elements is present. The crushing of the skull has caused considerable fracturing and disarticulation. The stoutness of the premaxillae, together with the presence of large tusks in this region, has caused these elements to be partially overturned and separated from the roofing bones posterior to them. The upward tilting of the sides of the skull into the horizontal plane has separated the lacrimals of both sides from the prefrontals, and on the left side has separated the "cheek" elements—squamosal and quadratojugal—from the table, and the left parietal, as well as the "table" elements posterior to it have been pushed some distance to the rear, together with the left "cheek".

In figure 3 I have attempted to articulate the roofing series in natural relations. Since, however, the palatal structure is almost unknown, I have been unable to determine the true width of the skull and consequently have been forced to restore the whole roof in an unnatural horizontal plane (fig. 3). As a result, the articulation between elements is to some extent distorted; more important is the fact that this type of restoration makes the skull appear considerably broader than it actually was in life.

The length, as restored, from snout to the back edge of the skull table, is 128 mm. The general proportions of the skull (allowing for the artificiality of the apparent width) are those of a moderately long and rather narrow structure. The orbits, apparently typically circular in outline, lie well toward the front of the skull, giving a relatively short face and a much elongated postorbital segment. The skull table is broad; on either side the cheeks slant backward gently toward the jaw articulation. The area of junction of cheek and table is disturbed on both sides. That the suturing was not too tight between the two regions is demonstrated by the clean break between cheek and table seen on the left. There was obviously little or no development of an otic notch.

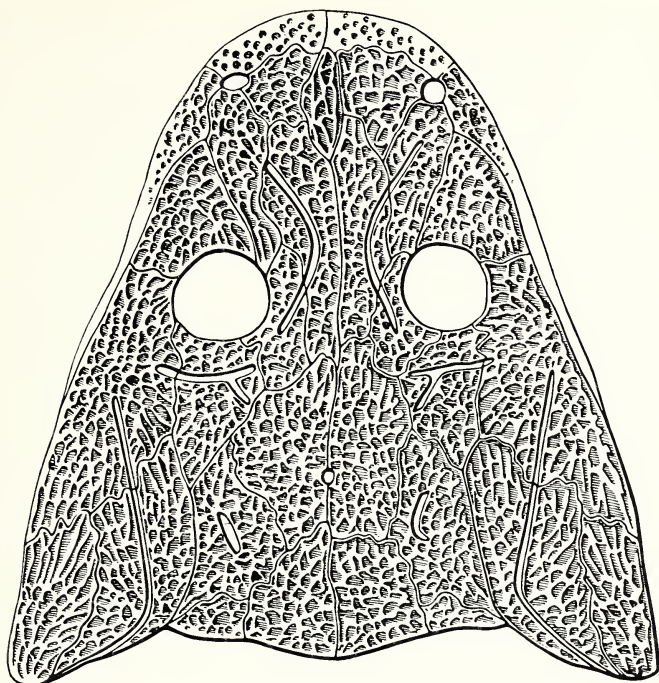


Fig. 3. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. The skull roof restored; the elements are shown as if all were in a horizontal plane, and hence the true width is exaggerated, $\times \frac{2}{3}$.

The sculpturing is of a typical labyrinthodont type: essentially circular depressions surrounded by ridges near centers of ossification, gradually changing to a series of long ridges with intervening valleys in elements which extend some distance from the ossification centers. A considerable amount of the potential pattern of grooves for lateral line canals is present. The cheek line is seen extending backward and upward on the posterior part of the jugal and anterior part of the squamosal, and then curving downward posteriorly to disappear at the posterior edge of the cheek near the squamosal-quadratojugal suture. Of the longitudinal canals originally present on the skull table, there is to be found only a pair of short grooves on the supratemporals. The supraorbital lyrae are distinctly developed on postorbitals, jugals and prefrontals. A transverse post-

orbital canal, forked medially, is present on both postorbitals. There is no trace of a suborbital groove although it may have been present along the suture between the (disarticulated) maxillae and the elements dorsal to them. I have seen no interpretable traces of canals such as are found on the snouts of various other labyrinthodonts.

The premaxillae are stout elements whose outer edges are considerably thickened and curve strongly downward from the level of the snout roof to the upper jaw margins. The anterior ends of the maxillae are broadened and obviously thickened dorsally; they extend as slender tooth-bearing strips far back below lacrimal and jugal. The state of preservation makes it impossible to give details of the region of the external naris; apparently premaxilla, maxilla, nasal and prefrontal enter into its borders. The lacrimal appears to have been excluded. The nasals are short but broad. Between two areas clearly belonging to the pair of nasals is a median strip of bone which I was at first inclined to consider a broken-off fragment of one of the nasals. However, the sculpture pattern of this area shows no relation to that adjacent to it on either nasal, and I think it likely that we have here an internasal, a median unpaired element such as is found occasionally in other labyrinthodonts.

The frontals are broad anteriorly, but narrow posteriorly between the orbits. The parietals are well developed, laterally occupying (with the postorbitals) the area in which intertemporals are present in many early forms. Postparietals are large and elongate.

Of the circumorbital series, the lacrimals are large, essentially triangular elements broadly exposed along the anterior margin of the orbits and tapering anteriorly; they appear not to have reached the external nares. The prefrontals are elongate, narrow posteriorly but broadening anteriorly. They appear to have but barely entered the orbital margins anterodorsally. The prefrontals extend much farther forward toward the nares than is typical of labyrinthodonts generally. About opposite the anterior tips of the lacrimals there is a crack separating the regions definitely pertaining to the prefrontals from an area running forward toward the nares. I am none too certain of the identification of the element or elements present here. Possibly the maxilla may extend medially here; possibly part or all of this area may constitute an external exposure of a septomaxilla (not otherwise identifiable in the specimen). It seems, however, more probable that we are dealing with a still further extension of the prefrontal.

The upper margins of the orbits are formed by the postfrontals, narrow anteriorly but broadening posteriorly where they extend some distance back of the orbits to reach the parietals. The post-orbitals are elongate anteroposteriorly, in conformance with the general elongation of the postorbital region of the skull; they taper posteriorly to terminate between supratemporal and squamosal. The jugal is the largest in area of the dermal roofing elements, covering most of the anteroventral area of the "cheek" and extending forward broadly beneath the orbit to the lacrimal.

Of the lateral elements of the skull table, the presumably primitive intertemporal is absent. The supratemporal is a large element, its anterior end lying between parietal and postorbital; posteriorly the supratemporal tapers laterally to a point close to the otic notch region. In temnospondyl fashion the tabulars are small, bounded anteriorly by the supratemporal and medially by the postparietal; there is, of course, no tabular-parietal contact. The squamosal is broad, and rather elongate; and the quadratojugal well developed. Although the articulation of squamosal with the skull table is obviously relatively loose, as noted earlier, there can be seen a flange of the squamosal which ran medially underneath the supratemporal.

It would be an extremely difficult task to remove the skull from the thick block of impure limestone in which it is embedded; in consequence little can be said of the palate, of which a few glimpses can be had through the orbits and broken areas of the skull roof. Part of the transverse flange of the left pterygoid has pushed up to the surface in front of the left squamosal, and portions of the anterior rami of the pterygoids are visible through the two orbits. In the left orbit is seen in dorsal view the somewhat thickened margin of the bone bordering the interpterygoid vacuity. On the right the bone has apparently been broken and displaced, so that the palatal surface of the same area is seen, the margin toward the interpterygoid vacuity bearing a band of small denticles.

As mentioned above, the right jaw ramus is concealed by the skull except for the articular region. On the left the block exhibits a considerable part of the ramus, including most of the dentary and parts of angular and surangular. A posterior fragment of this jaw, removed from the block during preparation, is shown in figure 4.

Much of the dentary is visible on the left jaw ramus. At mid-length of the bone there are teeth of labyrinthine structure and modest height, spaced at intervals of about 5 mm, with frequent

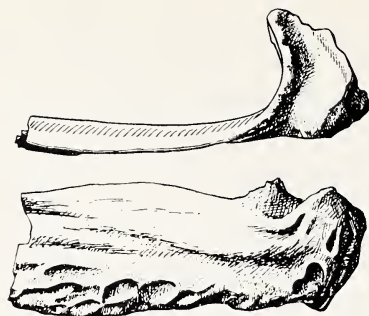


Fig. 4. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Left articular region and partial surangular in dorsal and lateral view, $\times 1$.

empty sockets in alternate positions. As expected, tooth size and spacing decrease posteriorly. A large tooth, with a length of about 9 mm, is seen projecting downward from the posterior margin of the left premaxilla. The right premaxilla has been broken off and overturned, revealing the presence here of several large tusks, grooved in labyrinthine fashion, and with estimated lengths of well over a centimeter. Two are broken off and one or both of these may have been parasymphysial teeth of the lower jaw. One however, is definitely attached to the premaxilla — a most unusual situation for a large tooth of this sort.

Postcranial skeleton: Much of the vertebral column is present, but disarticulated; as noted above, a considerable series of vertebrae of the anterior part of the trunk is represented by materials posterior to the skull on the main block (fig. 5); a second block carries a series presumably from the posterior part of the trunk (fig. 6). The vertebral structure is typically rhachitomous. On both blocks there are numerous intercentra; a total of about 30 are clearly visible. They are stout structures although in many cases broken in two by crushing. They have a typical crescentic shape, as seen in end view; broad below, with an anteroposterior dimension of 5 to 7 mm, they taper upward on either side to form nearly a semi-circle. Although moderately thick ventrally, there nevertheless remains a large cavity for the presumably persistent notochord. The curvature of the intercentra shows the diameter of the column to have been about 20 mm. The pleurocentra are less well preserved, but can be seen to have been the typical rhachitome wedge shape. A relatively few neural arches are visible. The spines are low, with

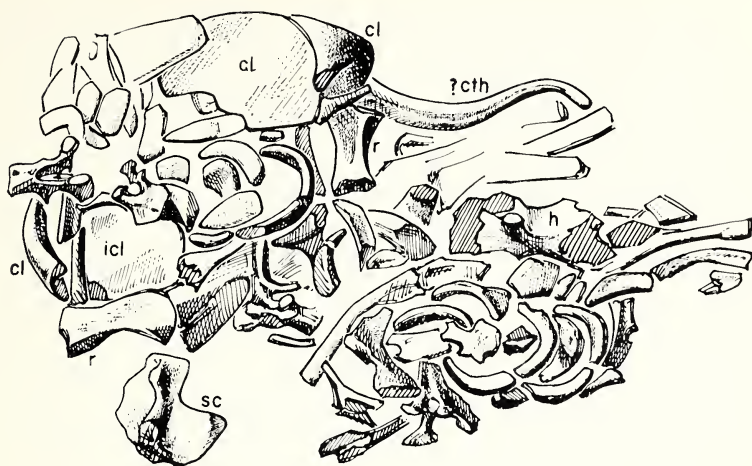


Fig. 5. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Postcranial remains present on main block: cl, clavicles; ?cth, possible cleithrum; h, humerus; icl, interclavicle; r, radius; sc, left scapulocoracoid, $\times \frac{2}{3}$.

the greatest height observed about 15 mm above the level of the zygapophyses, but are stoutly built, with transverse widths of several millimeters and anteroposterior dimensions of 5 to 7 mm. The zygapophyses diverge moderately on either side of the arch base, the width across them being 7 to 9 mm. On either side, the arch bases send broad processes down and outward ending below in horizontal surfaces for rib articulation. Scattered ribs are present; the longest seen has a length of about 40 mm. The slender shafts are nearly straight; the heads are expanded in triangular fashion.

I have not figured the abdominal scales, but a plentiful supply is present below each of the two series of vertebrae. They have the typical labyrinthodont oat-grain shape, and are generally about 10 mm in length.

As noted earlier, there was found with the specimen most of an appropriate series of limb and girdle bones (fig. 7). Those present appear to pertain to a single individual. All are of small dimensions for an animal with a skull of this size, indicating feeble limbs and an obviously aquatic habitat. As an indication of size, I may note that the femoral length is only about 25 percent of skull length, whereas in *Eryops* this figure averages about 35 percent, and in



Fig. 6. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Disarticulated elements — neural arches, intercentra, pleurocentra, ribs — pertaining to posterior part of trunk, $\times \frac{1}{2}$.

Cacops about 55 percent. On the other hand, members of the *Trimerorhachis* group, which are known from the Pennsylvanian and early Permian, are, like the present form, small limbed. Associated materials are none too common, but in this group femoral length appears to be rather less than 25 percent of skull length. At first sight, the limb and girdle structures in the present specimen appear to be generally comparable to those of trimerorhachoids.

The dorsal ends of both clavicles are visible behind the skull in the main block, projecting upward in typical tapering fashion. Their vertical position is due to their possession of expanded lower portions lying in the plane of the block surface; the blade of the right clavicle is exposed, that of the left concealed. I have not identified cleithra, although a long slender structure lying behind the right side of the skull may be such an element. A portion of the presumably expanded interclavicle is visible near the left clavicle. A single scapulocoracoid of the left side, seen from the inner sur-

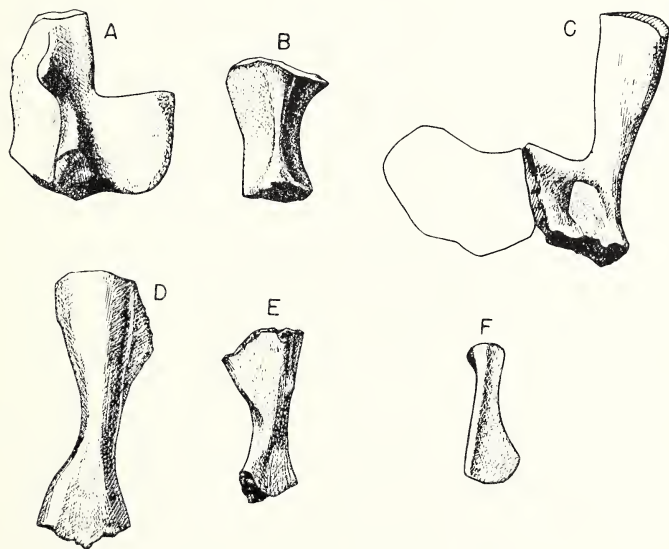


Fig. 7. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Limb and girdle elements. A, left scapulocoracoid, inner surface. B, right radius, flexor aspect. C, right ilium; ischium (seen only from inner surface) in outline. D, right femur, dorsal aspect. E, left tibia, extensor aspect. F, left fibula, extensor aspect, all $\times 1$.

face, is preserved adjacent to the left clavicle. As in trimerorhachoids, most of the coracoid plate and scapular blade is unossified; the scapulocoracoid as preserved includes only the general region of the supraglenoid buttress. The preservation is poor, and I am unable to determine whether or not the typical supraglenoid foramen was present. There are remains of both humeri, but little can be made out regarding their structure. Both radii are present; they are short but broad elements about 19 mm long and in general resemble the corresponding elements of *Eryops*. The lateral margin is thin. Posteriorly, toward the median side, there is a sharp longitudinal ridge. The upper end is very broad, with a width of 11 mm; the distal width is about 8 mm. Ulnae are not well preserved, and I have not identified elements of the manus.

Both ilia are present: the right well preserved, the left imperfectly. The shape is that seen in many later rhachitomes, with a tall vertical blade, and no trace of a posterior process (not even the slight spur seen in *Eryops*). There is a typical supra-acetabular buttress. The right ilium has a total height of 30 mm. The two ischia are present. Both are seen from the concave featureless inner surface; their greatest lengths, from acetabulum to distal end, are 24 mm and 20 mm, as preserved. There is no trace of a pubis; very probably, as in various other amphibians, this bone failed to ossify.

Of hind limb elements, the femur, tibia and fibula of the left side were found associated with one another and with the left ilium; the right femur and tibia were found isolated. The left femur has a length of 40 mm; the right, apparently incomplete distally, is 35 mm long. As in temnospondyls generally the head is expanded anteroposteriorly and thin dorsoventrally. From the articular surface of the head, an unfinished surface runs downward and distally along the outturned margin of the shaft for some distance, to be continued by a pronounced ridge which extends down the anteroventral margin of the shaft to terminate at the ventral distal midpoint. There is a typically gentle groove distally between the two slightly convex condyles. There are, as usual, two distal condylar facets for the tibia, the distal face of the bone giving the appearance of a thickened V, with an apex ventrally at the termination of the ventral ridge.

The two tibiae measure 22 and 21 mm in length. As with the radius, we are dealing with a short but stout element. The head is broadened to about 11 mm for apposition to the two femoral con-

dyles; the medial portion of the head is much the thicker of the two areas, with a depth of 6 mm. Below the medial head there is a slight development of a cnemial rugosity and crest. On the flexor aspect below the head there is a low, short but rugose longitudinal crest (a somewhat similar structure is present in *Eryops*). Below the head, the bone contracts, with a pronounced lateral convexity, to a short shaft and then, twisting somewhat laterally, expands to a distal articular surface clearly divided into separate areas for intermedium and fibulare. The distal end of the bone has a width of about 9 mm; the articular face is broadest on the facet for the fibulare, measuring here 4 mm. Except for lesser development of a cnemial crest, the whole structure of the bone resembles that of *Eryops*.

The left fibula is 18 mm long as preserved. Its proportions are those of early tetrapods in general. The upper end is about 3 mm wide; the broadened lower end has a width of about 7 mm. There are no identifiable remains of the pes.

DISCUSSION

That the amphibian here described was primarily a water-dwelling form rather than one leading a truly amphibious existence, seems clear from the small limbs, which were obviously incapable of supporting the body and heavy head on any extensive forays onto land, and from the developed series of grooves indicating a functioning lateral line system. A primarily aquatic existence in early Carboniferous amphibians generally is to be expected (the rather well developed limbs of ichthyostegids are a puzzling exception) in the seeming absence of a terrestrial food supply of animal nature before the radiation of insects in the Pennsylvanian.

Of greater interest, however, is the determination of the systematic position of this Mississippian form and its position in labyrinthodont evolution. Previously the only known Lower Carboniferous temnospondyls had been the obviously aberrant loxommids. We have here a form with orbits of normal shape, rather than the peculiarly elongate openings of the loxommids, and I fondly hoped at first, that the present form might prove to be a "generalized" rhachitome, close to the ancestor of the abundant rhachitomous amphibians of the Pennsylvanian and early Permian.

This, sadly, proves not to be the case. Typical later rhachitomes (except for short-skulled types) have orbits posterior to the mid-point of the skull length; here the eyes are well forward, with a relatively short face and a long postorbital region. A shortness of face combined with relatively small limbs suggests the trimero-rhachoid rhachitomes — a group which, although off the main line toward typical advanced rhachitomes and stereospondyls, nevertheless must have branched off at an early and primitive stage, since they preserved the primitive movable basal articulation of brain-case and palate and retained the intertemporal element. When, however, the skull was reassembled, this possibility disappeared, for there is no intertemporal.

Further thought and search led to the true but unexpected determination of the specimen's position. We have here a predecessor of the Colosteidae, a small group of Pennsylvanian temnospondyls of problematical relationships, whose members (*Erpetosaurus* and *Colosteus*) were described by Romer (1930) and by Steen (1931).

In every known regard the present form shows agreement with the two colosteid genera. The general skull proportions with a short face and a long postorbital region, are identical. Here, as in *Colosteus*, but in contrast to typical labyrinthodonts, there is no development of a marked otic notch. The pattern of the lateral line canals in our specimen is similar to that seen in *Colosteus*, except that the anterior portions of the system are not as well developed (as far as can be determined) as in the Pennsylvanian forms. Here, as in the colosteids, the lacrimal enters broadly into the orbital margin and tapers anteriorly, whereas in typical temnospondyls this bone enters the orbit only over a short stretch and is often completely excluded. The remarkable forward extension of the prefrontal found here is also characteristic of colosteids, and contrasts with the situation found in most labyrinthodonts. The pattern here of the long post-orbital segment of the skull (with the intertemporal absent) agrees well with that of the colosteids. To some degree a similar pattern is present in other temnospondyls in which the posterior part of the skull is lengthened, but the high development of postparietals and supratemporals, in contrast with much reduced tabulars, is notable.

It is obvious that in this new form the palate, although little of it is visible, was widely open, as in colosteids, and one may expect that here, as in that family, the movable basal articulation of brain-case and palate had been preserved. The most definitive point of

resemblance has to do with the presence, both in our form and in the colosteids, of large tusks near the tip of the snout — a situation unknown elsewhere among temnospondyls. The distribution of the large anterior teeth in *Colosteus* is not known in detail, but in *Erpetosaurus*, as figured by Steen (1931, figs. 4, 5) there are large tusks on the premaxilla, and in the present specimen at least one such premaxillary tusk is present.

Our new form, then, is definitely attributable to the Colosteidae. It is of interest in showing that this family, formerly known from the Pennsylvanian alone, is of great antiquity. But such attribution does not place it with any degree of assurance in the general picture of temnospondyl radiation, for the colosteids are themselves a problematical group. When the ichthyostegids were first described by Säve-Söderbergh (1932) I jumped to the conclusion, based on the general skull pattern, that *Otocratia* of the Mississippian and the colosteids of the Pennsylvanian were ichthyostegid relatives (Romer, 1947). The assumption that *Otocratia* is indeed related seems to be confirmed by the finding of ichthyostegids with comparable otic peculiarities (Jarvik, 1952), but that the colosteids are also ichthyostegids is very doubtful. Apart from general skull proportions and the loss of the intertemporal, there is at present no reason to claim relationships, and it seems more probable that the colosteids were, rather, an early offshoot of the Rhachitomi, paralleling the trimerorhachoids in skull proportions, small limbs, retention of a movable basal articulation and opening up of large interpterygoid vacuities, but differing in loss of the intertemporal.

Our present specimen does not, thus, furnish us with a potential ancestor of the typical rhachitomes of later times. But the presence in the Mississippian of such an unusual type, together with the equally aberrant loxommids, indicates that the radiation of the Rhachitomi was well under way in early Carboniferous times. Should future exploration, hopefully, result in additional finds of Mississippian labyrinthodonts, we may expect that there will be found in the faunal assemblages not only representatives of progressive stages in anthracosaurian evolution but also specimens demonstrating an active radiation of early rhachitomes.

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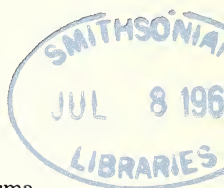
NUMBER 7

A NEW AMIOID FISH FROM THE UPPER CRETACEOUS OF KANSAS

DAVID H. DUNKLE

ABSTRACT

The partial skeleton of a small fish from the Niobrara Formation (Upper Cretaceous) of Kansas possesses a hemiheterocercal caudal fin, scales of rounded amioid type and other characteristics denoting a new holostean described as *Paraliodesmus guadagnii* gen. et sp. nov.



INTRODUCTION

There is a meagerness of published information about the diminutive members of the paleoichthyological faunas of the classic Upper Cretaceous formations of North America, coupled with a lack of demonstrable systematic diversity among these forms. This is quite evident when comparison is made with records from equivalent strata in other parts of the world.

Prompted by the mode of occurrence of *Leptecodon* (Stewart, 1900) and *Kansius* (Hussakof, 1929) which are preserved in the interiors of the shells of *Inoceramus grandis* (Conrad), this writer and G. Donald Guadagni made routine examination of eroding specimens of this pelecypod while collecting in the Niobrara Formation of western Kansas during the summer of 1954. The result of the search was recovery of numerous additional specimens of the small berycoid *Kansius* as well as one unfamiliar skeleton of modest size. Although incomplete, the latter specimen possesses an abbreviated heterocercal caudal appendage, scales of rounded amioid type and other characteristics here interpreted as denoting a previously unknown fish of holostean affinity. It is suggested that future search of this sort might well add appreciably to knowledge of a little-known faunal segment of the Kansas "Chalk".

I am indebted to the Smithsonian Institution for the privilege of making this study. Dr. Colin Patterson of the British Museum [Natural History], London and Dr. Richard Lund of the Carnegie Museum, Pittsburgh, were gracious in making pertinent comparative materials available for examination. The illustrations represent the work of two members of the staff of the United States National Museum: Lawrence B. Isham prepared the drawings and Jack Scott made the photographs.

SYSTEMATIC PALEONTOLOGY

Order AMIIFORMES Hay, 1929

Suborder AMIOIDEI Schlosser, 1934

Family ?CATURIDAE Koken, 1911

Genus **PARALIODESMUS** gen. nov.

PARALIODESMUS GUADAGNII¹ sp. nov.

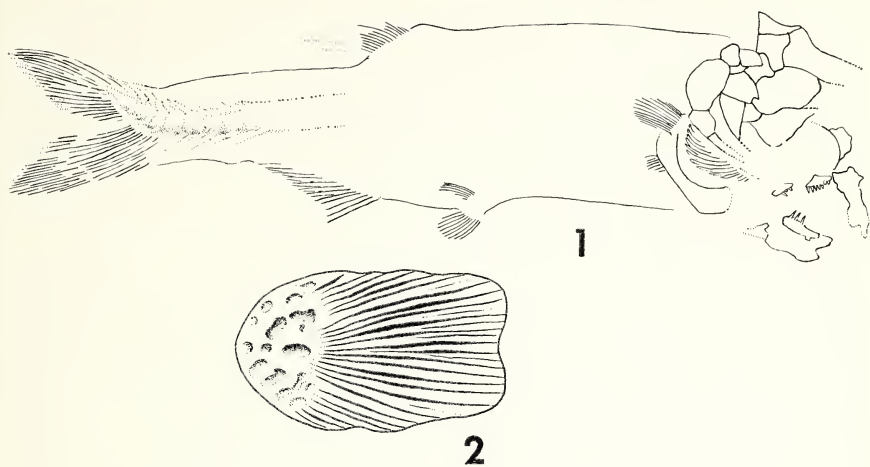
Pl. 1, figs. 1-3

Diagnosis for genus and species: An actinopterygian fish of holostean affinity which differs from any of the more comparable members of the families Caturidae and Amiidae in the following combination of characteristics: Dermal bones of the skull exceptionally thick and with a noticeably coarse rugose ornamentation; notochord persistent; dorsal fin originating remotely behind the pelvics and largely opposed to a long-based anal; caudal fin equilobate, deeply cleft and of apparent caturid internal structure; fins without evidence of fulcra except for spinelets of accumulative length in advance of both upper and lower lobes of the caudal fin; scales minute and of rounded amioid type.

¹ Named in honor of Mr. G. Donald Guadagni, codiscoverer of the holotype.

EXPLANATION OF PLATE 1

Figs. 1-3. *Paraliodesmus guadagnii* Dunkle, holotype, U. S. N. M. 21083.
1. Habit sketch of specimen, $\times \frac{2}{3}$; 2. Sketch of rounded scale, $\times 18$ (approx.);
3. Photograph of specimen, $\times \frac{2}{3}$.



Holotype: United States National Museum no. 21083, a fish preserved in part as an impression.

Horizon and locality: Smoky Hill Member of the Niobrara Formation (Upper Cretaceous) in sec. 36, T. 15 S., R. 31 W., Gove County, Kansas.

DESCRIPTION

Post-depositional compression of the *Inoceramus* valves with consequent comminution of the enclosed skeleton and subsequent exposure of the anterior half of the body has largely obliterated fine structural detail. Clearly observable, however, is the outline of an entire fish shown by (1) an impression of the left anterior side of the body on the internal surface of the lower shell and (2) the right aspect of preserved posterior scales, fins and axial structure which were protected prior to discovery by portions of the upper shell that had remained in place during weathering. An elongate fusiform fish is indicated with a maximum body depth of 35 mm, a stout caudal pedicle of 15 mm depth, and head and opercular apparatus occupying 40 mm of a total overall length approaching 170 mm.

The head is obliquely crushed and is seen in ventrolateral aspect. Only remnants of the skull bones remain but these are of remarkable thickness, with coarse and radiating rugose ornamentation. Whether or not an external covering of enamel is retained on the cranial elements and scales has not been definitely ascertained, but its presence is suspected. The suspensorium would appear to have been vertical and the mouth terminal, with wide gape. The premaxillaries are in contact with each other mesially and are succeeded dorsally in the snout by a reduced rostral bone which is broader in front than long. Preserved fragments of the right maxillary show an elongate element, somewhat deepened behind, with a straight oral border. The separate bones of the mandibles cannot be discerned. However, the dentary portion is relatively low anteriorly, progressively deepening to a coronary eminence posteriorly. These visceral elements all bear a single labial row of robust teeth. Those of the upper jaw are particularly stout and strongly recurved. Dentary teeth are, in comparison, high, thin and styliform. Part of a presumed splenial exposed beneath one of the lower jaws displays a random arrangement of minute denticles.

The number and arrangement of the opercular bones are characteristic of the amioid fishes. The operculum is slightly the larger element of the series with rounded posterior margin and antero-ventral notch receiving an ascending process of the suboperculum. The branchiostegal rays, in typical fanned pattern, are narrow and numerous.

The notochord is persistent to its tip in the epichordal lobe of the equilobate and noticeably notched caudal fin. The downcrushing of scales over the expanded proximal processes of opposing neural and haemal arches vaguely suggests segmentation of the notochordal axis posteriorly, but no evidence of central ossifications can be detected. If indeed such are present under the scale cover, they must be very weak. Neural and haemal structures are acutely recumbent upon the notochord throughout the caudal region. The development of the posterior haemal spines is poorly visible. While somewhat expanded, none that can be seen appears larger than another. Nevertheless there is a definite overlap of the clustered and forked proximal ends of the principal rays of the upper lobe of the caudal fin across several of the posterior uptilted hypural bones as in *Caturus* (Lund, 1967).

The dorsal fin appears to have been about as long as high and originates well behind the midlength of the specimen, posterior to the plane of the pelvic fins and only slightly anterior to the origin of the lower, longer-based anal.

The position of the pectoral fins has been distorted by the oblique crushing of the head. It seems probable, however, that they were somewhat elevated on the sides of the body. They are indicated to have been larger than the pelvics. The separation of the paired fins is about twice the distance between the pelvics and the anal fin.

The forward edges of the upper and lower lobes of the caudal fin display a number of undivided rays of posteriorly accumulative length. These may also be present on the other fins, but evidence of fulcral scales of more typical chondrosteian or semionotoid form is absent.

Scales of this fish are rounded, narrower apically than basally, and only about 2 mm in length. The center of growth and exposed portion of the scale, as marked externally by a few tubercles and coarse, radiate rugae, is far apical and very short. The basal covered portion of each is of much greater area and displays fine, more

or less parallel striae which radiate to the upper, lower and anterior margins of the scales.

DISCUSSION

Known Cretaceous fishes of holostean stock are relatively few in number. Among these, *Paraliodesmus* shows greater similarity only to representatives of the families Caturidae and Amiidae. It is distinguished from the essentially contemporaneous *Lophiostomus* and *Neorhombolepis* (Woodward, 1895), and *Enneles* (Santos, 1960) by scale type and size. Closer comparability of the characters elucidated are in fact seen with the older and better known Jurassic genera *Caturus* and *Liodesmus*. It differs most obviously from the latter two in fin position and the thickness and coarse ornamentation of the skull bones. Caudal structure suggests tentative reference of *Paraliodesmus* to the family Caturidae rather than to Amiidae. Such assignment necessitates assumption that the absence of fulcra occurred independently in a number of phyletic lines, as did the rounding and reduction of the scales (Schultze, 1966).

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THE CLEVELAND MUSEUM OF NATURAL HISTORY

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NUMBER 8

TREMATOPS STONEI SP. NOV. (TEMNOSPONDYLI:
AMPHIBIA) FROM THE WASHINGTON FORMATION,
DUNKARD GROUP, OHIO

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ABSTRACT

Trematops stonei, a new species of this genus of temnospondylous, labyrinthodont Permian amphibian, is described and figured. The specimen upon which the description is based was found in the Creston Shale, Dunkard Group, Lower Permian at Marietta, Ohio. This genus, along with *Melanothyris* (previously known from the Dunkard), and *Dimetrodon* and *Diadectes*, recently obtained from a channel-fill deposit at Belpre, Ohio, indicate the presence of a terrestrial component in the Early Permian faunas of this region. This part of the faunal complex is rarely represented in the usual pond-lake deposits of the Dunkard Group.

INTRODUCTION

The vertebrate fossils of the Dunkard Group have become fairly well known through the studies of Moran (1952), Romer (1952) and Beerbower (1963). Extensive collections have come from Ohio, Pennsylvania and West Virginia. These include many as yet undescribed specimens so that faunal considerations, based as they must be upon published information, are necessarily somewhat incomplete. Among the collections of the Cleveland Museum of Natural History is the skull described in this paper. It is of sufficient interest that its description cannot await studies of other collected but undescribed materials.

Over the areas in which the Dunkard occurs, a more or less continuous sequence of fossiliferous beds includes deposits formed in the Late Pennsylvanian (Stephanian) and Early Permian (Autunian). Finds of vertebrate remains in these beds are widely scattered geographically and the fossils are for the most part fragmen-



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tary. Outcrops are limited by the heavy cover of vegetation over the area, and remains have in large part come from roadcuts or persistent exposures created by resistant limestone. Nevertheless, representatives of nearly 30 genera and species have come from the Dunkard portion of this sequence, comprising several groups of fishes, amphibians and reptiles. These, for the most part, are, at a generic level, similar to the Late Pennsylvanian and Early Permian vertebrates found in the better known areas of the Midcontinent region, including northcentral Texas, Oklahoma, Kansas, New Mexico, Colorado and Utah. In addition, there are striking similarities to the Late Pennsylvanian vertebrates from the Oakwood locality of Illinois (see Olson, 1946). A few genera, the best known of which are *Diploceraspis* and *Megamolgophis*, are absent from Midcontinent collections.

Both the Pennsylvanian deposits (Conemaugh and Monongahela) and the Permian Dunkard are of the general "coal measures" type, including sandstones, shales, clays and freshwater limestones, along with coal. The gray dolomite and shale series of the Wellington Formation of northcentral Oklahoma, except for the absence of coal, approaches this depositional pattern most closely of Midcontinent vertebrate-bearing formations. The predominant sediments in both areas indicate deposition in shallow waters along the shores of large freshwater lakes. In both areas occur sandstones and conglomerates deposited by current action. From such deposits, more commonly in Oklahoma than in the eastern United States, have come some fragmentary remains of kinds of animals not usually encountered in the typical lake beds.

It is from such a deposit that the specimen that occasioned this paper came. In February, 1969, Reed W. Irwin, a member of a Marietta College field party investigating local Dunkard stratigraphy under the direction of Dr. Dwayne D. Stone, discovered the specimen. It is part of a growing collection of Dunkard vertebrates in the Cleveland Museum of Natural History. The specimen came from the upper, green to gray beds of the Creston Shale (red beds) of the Washington Formation, Dunkard Group, of Ohio. David Dunkle turned the specimen over to me for study. It had been excellently prepared by Peter R. Hoover. The illustrations were prepared by Eleanor Daly. I here express my appreciation to each of these persons for their contributions to this study. The work was supported in part by National Science Foundation Grant GB 13910.

SYSTEMATIC PALEONTOLOGY

Class AMPHIBIA

Subclass LABYRINTHODONTIA

Order TEMNOSPONDYLI

Family TREMATOPSIDAE Williston, 1910

Genus **TREMATOPS** Williston, 1909**TREMATOPS STONEI**¹ sp. nov.

Figs. 1, 2

Diagnosis: A moderately large species of *Trematops* with length of skull of holotype (only known specimen) about 140 mm, as measured along the dorsal midline, slightly less than for known adult specimens of *T. milleri* Williston. Marginal maxillary dentition comprising relatively few, large, strongly labyrinthine teeth. Tusk and pit on palatine bone strongly developed.

Holotype: Cleveland Museum of Natural History 10969, a partial skull.

Horizon: Creston Shale (red beds) of the Washington Formation, Dunkard Group, Lower Permian, immediately below the Upper Marietta Sandstone.

Locality: Roadcut on Ohio Route 7, at Marietta, Washington County, Ohio, 0.7 mile southwest of U.S. Route 50A.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

Description: The principal features of the skull are as shown in figures 1 and 2. The specimen is somewhat distorted and the marginal portions, except forward from the midorbit on the left side, much of the palate, and part of the snout are missing. A typically trematopsid, large elongated narial fenestra is preserved on the left side. The braincase, basicranium, parasphenoid, sphenethmoid and interorbital-internasal septum are well preserved and show considerable detail. All of these structures conform very closely in form and size to those present in *T. milleri*.

¹ The species name is given in recognition of Professor Dwayne D. Stone of Marietta College, whose interest and inquiry about the specimen ultimately resulted, with his cooperation, in its acquisition by the Department of Paleontology of the Cleveland Museum of Natural History.

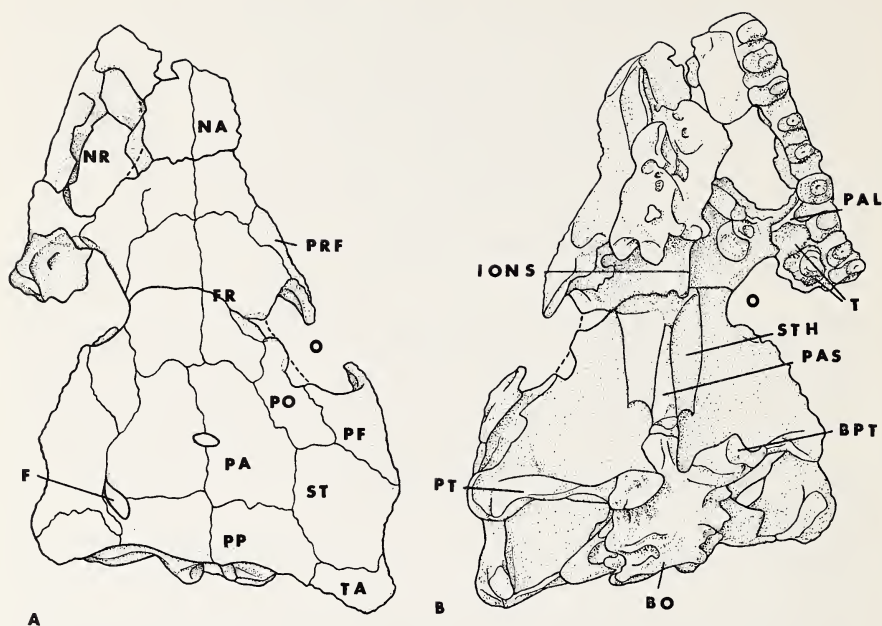


Fig. 1. The skull of *Trematops stonei* sp. nov., $\times \frac{1}{2}$. A. dorsal view; B. ventral view. Abbreviations: BO, basioccipital; BPT, basipterygoid process; F, fossa on parietal platform; FR, frontal; IONS, interorbital-internasal septum; NA, nasal bone; NR, naris; O, orbit; PA, parietal; PAL, palatine; PAS, parasphenoid; PF, postfrontal; PT, pterygoid; ST, supratemporal; STH, sphenethmoid; T, tusk and pit on palatine.

The dorsal platform and lateral dermal surface of the skull carry the usual reticulate, sculptured pattern found among the labyrinthodonts. Although the bone is riddled by small, mineralized fractures, the sutural pattern has remained moderately clear and the reconstruction in figure 1 is reliable. On the left side of the parietal shelf, a small, anomalous, elliptical fossa passes through the bone (F in figure 1A). It has well-formed, smooth finished edges. It will be noted in the figure that the sutural pattern in the vicinity of this opening is somewhat altered, showing that the fossa was formed early in ontogeny and that it interrupted normal bone growth. Whether it was a genetic defect or was induced by an early mechanical interruption of normal growth cannot be determined.

Assignment: Reference of this specimen to the family Trematopsidae poses no difficulties for it is similar in all gross features to the

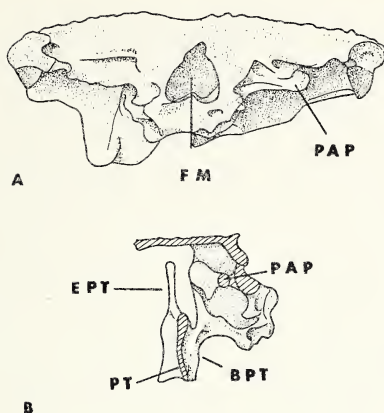


Fig. 2. *Trematops stonei* sp. nov., $\times \frac{1}{2}$. A. occipital view; B. braincase in lateral view, lateral dermal bones removed. Abbreviations: BPT, basipterygoid process; EPT, epipterygoid; FM, foramen magnum; PAP, paraoccipital process; PT, pterygoid bone.

best known members of this family, *Acheloma* and *Trematops*. The large, elongated external nares, the pattern of the dorsal and lateral dermal bones, the strongly deflected basipterygoid processes, which are fused to the pterygoids, the form of the braincase, including the high, slender epipterygoid, and the narrow cultriform process of the parasphenoid, which fails to meet the vomer anteriorly, are the primary bases for this relationship (see Olson, 1941).

Recently Vaughn (1969) considered the relationships of the families Trematopsidae and Dissorophidae. On the basis of his new genus *Ecolsonia*, which incorporates some features of dissorophids although it is clearly trematopsid, he provided strong support for the concept of close relationship between the two families. DeMar (1966) described *Longiscitula*, an animal which has an elongated, trematopsid-like narial opening, but is basically dissorophid in many features. This, like Vaughn's genus, indicates that the families are closely related but that they had undergone considerable divergence from an unknown stock which must have existed well prior to the Permian.

The only problem of generic assignment of *T. stonei* has been whether it belongs to the genus *Acheloma* or to *Trematops*, which, as discussed in an earlier review (Olson, 1941), are very similar. As

far as the structure of the skulls is concerned, the differences are such that they could be judged to be either of specific or of generic value. In instances where the structure is known, the frontal bone is shorter in relationship to the parietal in *Trematops* than in *Acheloma*, the tabulars are relatively larger, the nasals relatively longer and the squamosals relatively smaller. Postcranial differences are somewhat more definitive. Most important is the complete ossification of the hypocentra above the notochordal opening in *Trematops* and the incomplete ossification in *Acheloma*. In addition the coracoids are better ossified in *Trematops* and the scapular blade is erect in *Trematops* and reflected posteriorly in *Acheloma* (Olson, 1941). The significant postcranial differences, of course, are not applicable at present to placement of the new species.

On the basis of the relatively short frontal, the moderately large tabular and the relatively strong ossification of the braincase, the Dunkard specimen is referred to the genus *Trematops* rather than to *Acheloma*. It is considered to be distinct from *T. milleri*, which it most closely resembles in size and proportions, primarily on the basis of the marginal and palatal teeth. Although the full tooth row is not present in the Dunkard specimen, it is probable that the total number of marginal teeth did not exceed 20. The teeth preserved in *T. stonei* are robust except for the most posterior three, which show rapid reduction in size. This contrasts somewhat with the teeth of *T. milleri*, which are comparably large only at the level of the anterior part of the orbits and the posterior part of the naris. In addition, the palatal tusk on the palatine bone of *T. stonei* is very strong compared with that of other species of *Trematops*. These are minor morphological differences and the few known specimens do not indicate what role variation may have played. They do, however, offer a morphological basis for separating the one known specimen of *T. stonei* from those of *T. milleri*, a separation that is suggested as well by the significant time interval between the two, the one coming from the very beginning of the Permian and the others from Clear Fork beds (Arroyo Formation) in the middle Leonardian.

Measurements in millimeters of the skull dimensions of the holotype and only known specimen of *Trematops stonei* sp. nov. C.M.N.H. 10969 are as follows:

Skull length, along dorsal midline	140
Parietal length, along midline	33 (left) 37 (right)
Postparietal length, along midline	17 (left) 13 (right)
Frontal length, along midline	38
Skull width, least width between otic notch margins on skull platform	86
Narial length, maximum	37

OCCURRENCE AND SIGNIFICANCE

The specimen of *T. stonei* sp. nov. was found near the top of the "red shale" interval, the Creston Shale, between the lower and the upper Marietta sandstones of the Washington Formation. Over the years the status of the Washington as a formation or a more comprehensive stratigraphic unit has been debated (see Hennen, 1911, McCue, et al. 1948, Hickock and Moyer, 1940, Moran, 1952, and Nace and Bieber, 1958). For the purposes of this study the conceptual differences involved in these discussions are unimportant and for simplicity the Washington is considered to be a lithologically complex formation. The thickness of the formation ranges from about 250 to 400 feet. Included, along with the sandstones mentioned above, are five coals and four limestones.

The Creston Shale ranges between 35 and 60 feet in thickness and lies between the Middle Washington Limestone below and the Washington "A" Coal above. The latter is a reworked coal in the area where the specimen was recovered. Overlying it is the Upper Marietta Sandstone which has channeled to varying degrees into the underlying beds. This sequence represents a variety of environments of deposition among which some, such as the Creston Shale, give indications of being in part terrestrial. The only other vertebrate remains from the Creston are a fragment of a spine of *Edaphosaurus* found at Marietta, Ohio, by Stauffer (Stauffer, 1916, Stauffer and Schroyer, 1920, Moran, 1952) and coprolites reported by field parties from Ohio University. All specimens have come from near the top of the beds.

The vertebrates add little to an understanding of the age of the deposits. The Washington beds form the lower part of the Dunkard and are generally placed as very early Permian (Moran, 1952)

or possibly as bridging the Stephanian-Autunian boundary (Dunbar, et al. 1960, Beerbower, 1963).

The most fossiliferous locality in the Washington that has been fully described to date is locality 6 of Moran (1952) located in the SW $\frac{1}{4}$ sec. 18, T. 3 N., R. 4 W., Monroe County, Ohio, about 40 miles northwest of Marietta. The fossils came from a series of limestones and shales which ranges from 2 to 4 feet in thickness. The beds lie about 7 to 10 feet below the Washington "A" Coal and are thus more or less comparable in stratigraphic position to the site from which *T. stonei* sp. nov. was taken. As identified by Romer (1952) this assemblage includes:

Dittodus sp. (= *Xenacanthus* sp.)

Sagenodus cf. *S. periprion*

Eryops cf. *E. megacephalus*

"Branchiosaurs"

Rhachitomi indet.

Diploceraspis *burkei*

Lysorophus *dunkardensis* (presence not certain)

Melanothyris *morani* (a jaw possibly pertaining to the genus and species)

Edaphosaurus cf. *E. boangeres*

?*Baldwinonius* *dunkardensis* (jaw fragment)

Collections made during the last few years have produced an extensive vertebrate assemblage from Belpre, Washington County, Ohio. This has been reported by Hlavin, Windle and Wilcoxon (1968). A heretofore unpublished faunal list from this locality supplied by William Hlavin is as follows:

Ctenacanth-cladodont group (teeth and spines)

Xenacanthus sp.

cf. *Ectosteorhachis* sp.

Sagenodus sp.

Elonichthys sp.

Eryops cf. *E. megacephalus*

Rhachitomi indet.

Diploceraspis sp.

Lysorophus sp.

Megamolgophis sp.

Diadectes sp.

Edaphosaurus cf. *E. boangeres*

Dimetrodon sp.

Pelycosaurs, indet.

Some specimens from this site were kindly sent to me by Mr. Hlavin and these give some added insight into the vertebrates present at Belpre. A rhachitome, (probably *Eryops*), *Diploceraspis*, *Diadectes*, *Edaphosaurus* (cf. *E. boangeres*), *Ophiacodon* and *Dimetrodon* are readily identified in this assemblage. In addition a large vertebral centrum probably is from *Megamolgophis*, although it is not beyond the size range of the largest Texas and Oklahoma specimens of *Lysorophus*. Furthermore, a very large, rugose, tooth-bearing portion of the margin of the skull of a large labyrinthodont is present. This represents *Edops* or a very *Edops*-like amphibian.

The Belpre locality lies about 10 miles southwest of the Marietta *Trematops* locality, and the specimens were found directly above the Upper Marietta Sandstone. The bone-bearing deposit represents a channel-fill and is composed of pebbles up to 2 inches in diameter. The vertebrate remains were evidently washed in and, although they are well preserved, they are fragmentary.

The fossils at locality 6 of Moran (1952) portray a typical freshwater pond and pond-margin array. Throughout much of the Washington and the overlying Greene Formation such assemblages predominate. Beerbower (1963) in his discussion of the paleoecology of *Diploceraspis*, which covered most of the sites for which substantial samples were known, indicated the predominant environment as that of "lakes and ponds." The few identified stream channels, except the one at Belpre, have yielded mostly unidentifiable scraps. None of the fossil-producing beds described by Moran (1952) and Romer (1952) were formed by deposition in stream channels.

This has resulted in a strong bias in preservation of types of habitats, occasioned in large part, it would seem, by the fact that resistant limestones provide the bulk of the outcrops. Natural stream cuts and even road cuts in other materials are rapidly obliterated. It seems highly likely that, as in the Midcontinent area, more terrestrial environments existed adjacent to the standing waters. Fragments and a few more complete specimens from the Washington Formation have given indications of such environments. From Blacksville, West Virginia, *Melanothyris*, a small romeriid captorhinomorph, is indicative of a terrestrial habitat, although the specimens were preserved in limestone nodules.

Elsewhere specimens of *Lysorophus* are known, and *Megamolgophis* has come from one Washington locality. *Lysorophus* is quite certainly an aestivator and, on the basis of great similarity of structure, *Megamolgophis* probably was as well. The distinctions between the Dunkard *Lysorophus* specimens and those from Texas were based primarily on size, expressed in length of vertebral centra. It is now clear that the size ranges in the two regions completely overlap and that there is no adequate morphological basis for separation. The vertebrae of *Megamolgophis* are somewhat larger than those of the largest *Lysorophus* from the Texas area, with the average central length as noted by Romer (1952) of 15 mm, about 2 mm greater than the largest known from the Choza of Texas and the Hennessey of Oklahoma. There is, as far as the vertebrae are concerned, no reason to presume the habits to have been different. The skull materials referred with some hesitation to *Megamolgophis* by Romer (1952) indicate a quite different animal and, if the association is correct, may suggest a very different way of life.

If *Lysorophus* and perhaps *Megamolgophis* are indicative of aestivation, they suggest the existence of seasonality in the climate of the Dunkard area. It should be noted, however, that as yet no evidence of the commonly aestivating dipnoan, *Gnathorhiza*, has been reported.

Although much of the Belpre assemblage has the same general cast as that from locality 6 of Moran (1952), the presence of *Dimetrodon* and also of *Diadectes* suggests that somewhat different ecological circumstances may have contributed elements to the total assemblage. The large *Ophiacodon* at Belpre similarly suggests that at least partially terrestrial pond and stream margins were sources of parts of the faunal assemblage.

In this array of Washington specimens, however, even with such genera as *Diadectes*, *Ophiacodon* and *Dimetrodon* present, *Trematops* is something of an oddity. The genus is not a typical representative of pond or lake assemblages in the Texas-Oklahoma regions, where it is well known. *Acheloma* from the Wichita beds perhaps comes slightly closer to filling such a role, but even it was probably relatively highly terrestrial. *Trematops* in its typical occurrences is associated with dissorophids, *Seymouria*, captorhinids and *Dimetrodon*. It does not occur, except as possible fragments, in stream deposits or in typical pond deposits characterized by

Xenacanthus, palaeoniscoids, *Trimerorhachis*, *Eryops*, *Diplocaulus*, *Edaphosaurus* and, of course, the ubiquitous *Dimetrodon*.

The specimen of *T. stonei* in the Creston Shale of the Washington Formation gives very clear evidence, along with *Melanothyris*, of the existence of a truly terrestrial life zone in the mideastern region of the United States during the Early Permian. It would appear that the various faunal subgroups, well known in the mid-continent, occupying standing water, streams, margins of the ponds and streams and the low divides or "uplands" persisted far to the east from the places in which they were first recognized.

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SOME ORNAMENTED ERISOCRINIDS FROM THE AMES LIMESTONE

J. J. BURKE

ABSTRACT

Three new species of erisocrinid inadunate crinoids from the Ames Limestone, Conemaugh Group, Pennsylvanian, are described. All are ornamented forms. *Delocrinus brookensis* sp. nov. from Brooke County, West Virginia, is more specialized than *Delocrinus tulsensis* (Strimple) from the Desmoinesian of Oklahoma, but is probably a derivative of that species. *Endelocrinus pennsylvanicus* sp. nov. from Allegheny County, Pennsylvania, appears to be the largest Pennsylvanian representative of *Endelocrinus* and is also characterized by spine-bearing primibrachs. *Paradelocrinus decoratus* sp. nov. from Brooke County, West Virginia, in addition to being ornamented, is a relatively large species, but otherwise seems to be a fairly conservative member of the genus.

In a discussion that follows, the recent proposal by Knapp to remove from the Cladida forms with a dorsal cup having a basal concavity and include them in a new order, the Declinida, is opposed because adequate grounds for such action are not evident.

Ornamented crinoids representative of the family Erisocrinidae are fairly common in marine beds of the Conemaugh Group, Pennsylvanian, of the Allegheny region, and the three new species from the Ames Limestone described in the present paper represent only a few of the Conemaugh forms characterized by surface features such as nodes, granules, or a combination of the two. Unfortunately, ornamentation in many of these crinoids is quite variable, apparently undergoes modifications during ontogeny, and is often poorly preserved in fossil material. However, the specimens under description appear to represent mature forms, the ornamentation is fairly well preserved, and my specific distinctions are not based on ornamentation alone.

I wish to extend my appreciation to Mr. Bruce Frumker, staff photographer of the Cleveland Museum of Natural History, for the



photographs from which the illustrations were taken, and to my wife, Emily A. Burke, for aid in preparation of the manuscript and arrangement of the illustrations.

SYSTEMATIC PALEONTOLOGY

Family ERISOCRINIDAE Miller, 1889

Genus **DELOCRINUS** Miller and Gurley, 1890

DELOCRINUS BROOKENSIS¹ sp. nov.

Fig. 1

Diagnosis: Dorsal cup in general resembling that of *Delocrinus tulsaensis* (Strimple) but larger (width 23.4 mm) and higher (form ratio .34) with deeper basal impression, less prominent nodose ornamentation, and anal X more reduced in size.



Fig. 1. *Delocrinus brookensis* sp. nov. Holotype, Cleveland Museum 3912, from the Ames Limestone, Conemaugh Group, Brooke County, West Virginia. a, dorsal view; b, posterior view; c, ventral view, $\times 1$.

Holotype: Cleveland Museum of Natural History 3912, a complete dorsal cup.

Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Excavation (Tunnel Road Cut) for West Virginia Route 67 (lat. $40^{\circ} 14' 24''$ N., long. $80^{\circ} 35' 53''$ W.) near McKinleyville, Brooke County, West Virginia.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

Description: The dorsal cup of this species is low, truncate bowl-shaped, and of medium size. In dorsal view the cup appears sub-round, in ventral view pentagonal. The basal impression extends

¹ Named for Brooke County, West Virginia.

somewhat beyond midheight and occupies about half the diameter of the cup.

None of the stem is preserved. The infrabasals slope downward steeply, and flare outward slightly. They extend for nearly three-fifths the height of the basal impression. Proximally the curvature of the basals is moderate, but distally, along the sides of the cup, the curvature is more abrupt. Within the basal impression these plates are gently concave transversely, and even slightly concave at the basal plane, but become gently convex distally. Except for the posterior basal, which is longer than wide, the basal plates are slightly wider than long.

The radials are slightly less than twice as wide as long, have fairly steep slopes, and are slightly convex along their length except for a sharp incurvature distally to form a moderate forefacet. These plates are broadly convex from side to side, contributing to the sub-round outline of the cup in dorsal view. The articular facets show denticles on the outer ligament areas and the transverse ridges, prominent oblique fossae and broad intermuscular notches.

Anal X is relatively small, about a fourth longer than wide, strongly incurved distally and slightly concave from side to side proximally. It bears a single distal facet for articulation with a second tube plate.

The major ornamentation consists of prominent nodes, the largest of which are arranged in a festoon-like row bordering the forefacet of each radial. Below these, scattered nodes occur on the radials and on those portions of the basals that are part of the lateral wall of the cup. In addition to the nodes, fine granular ornamentation is distributed over most of the cup, including the proximal portion of the basals.

Linear measurements of the holotype, in millimeters, are given in the table below:

Height of dorsal cup	7.9
Width of dorsal cup	23.4
Ratio of height to width	0.34
Height of basal impression	5.0
Width of basal impression	11.5
Length of basal (raB)	8.9
Width of basal (raB)	9.2
Length of radial (aR)	7.3
Width of radial (aR)	12.9
Length of suture between basals	6.0
Length of suture between radials	3.2
Length of anal X	4.8
Width of anal X	3.6

Remarks: As the diagnosis indicates, this species resembles *Delocrinus tulsaensis* (Strimple, 1962). It is probably a direct derivative of the Oologah species and as such may be taken as an indicator of the rate of evolution in this line of crinoids from Oologah to Ames time.

Knapp (1969) advocates that the generic name *Delocrinus* Miller and Gurley be treated as a *nomen dubium* and the name of the genotype species, *Poteriocrinus hemisphericus* Shumard, 1858, a *nomen nudum*. In support of these proposals he notes that Shumard's types have been lost, regards Shumard's description as inadequate and indicates that no described specimens subsequently assigned to the species agree with the original description. However, I am in agreement with Moore and Plummer (1940, p. 253) in feeling that "the essential characters of the genus and its validity are not in doubt." Furthermore, although the species is probably a rare one, I think that the description will prove adequate to distinguish it, if additional specimens are discovered. In any case, as long as there is a possibility that topotype material may be found, *Delocrinus hemisphericus* (Shumard) has claim as a valid species.

In a previous paper (Burke, 1966) I regarded Strimple's (1961) proposed genus *Graffhamicrinus* as a synonym of *Delocrinus*, because it was based on surface ornamentation, a feature insufficient for generic distinction. Knapp (1969) recognizes *Graffhamicrinus* as a genus but (p. 363) emends it to include several other species previously included under *Delocrinus* "in which the proximal tips of the radial plates are visible in side view, the cups may or may not be ornamented, and in which the first primibrachs, which are axillary, may or may not bear spines."

As thus emended, *Graffhamicrinus* does not appear to me to have any better claim to generic distinction than it had previously. In this connection it is interesting to note that the measurements given by Shumard (1858, p. 221) for *Delocrinus hemisphericus* indicate that the proximal tips of the radials of that species are visible in side view.

Genus **ENDELOCRINUS** Moore and Plummer, 1940

ENDELOCRINUS PENNSYLVANICUS sp. nov.

Fig. 2

Diagnosis: A large species, near *Endelocrinus texanus* (Weller) in size (width of dorsal cup .21 mm) but cup higher (form ratio .36) basal impression nearly twice as deep, walls steeper, and plates ornamented with nodes and granules. Primibrachs spinose.

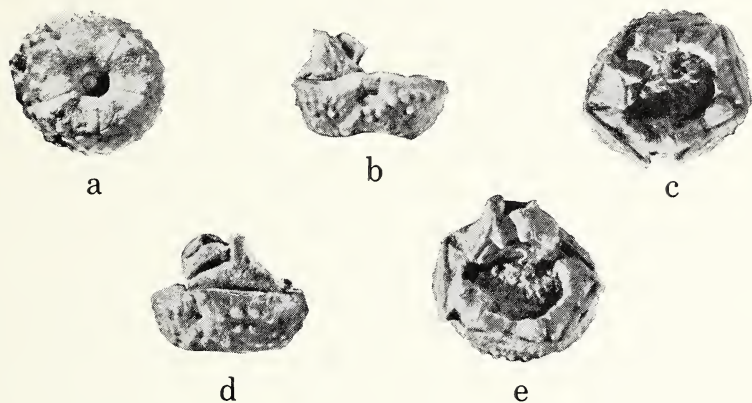


Fig. 2. *Endelocrinus pennsylvanicus* sp. nov. Holotype, Cleveland Museum 3913, from the Ames Limestone, Conemaugh Group, Allegheny County, Pennsylvania. a, dorsal view; b, posterior view; c, ventral view; d, E-ray view showing IBr₁, IIBr₁₋₂ (A ray on left); e, oblique ventral view showing articular facets of IBr₁ and IIBr₂, E ray, $\times 1$.

Holotype: Cleveland Museum of Natural History 3913, a dorsal cup with the first primibrach and two secundibrachs of the E ray attached.

Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Excavation at Holiday Park (lat. 40° 27' 46" N., long. 79° 42' 57" W.) Plum Borough, Allegheny County, Pennsylvania.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

Description: The dorsal cup is truncate bowl-shaped and of medium height. The vertical extent of the basal impression is nearly three-fifths the height of the cup, and the width of the impression is slightly less than two-fifths the width of the cup. The infrabasal circlet

shows a pentalobate central canal within the stem impression. The infrabasals are steep-walled, occupy more than half the height of the basal impression, and flare outward to the extent that they would be visible if the stem were attached.

The basals are about one-sixth wider than long. They flare steeply outward and downward from the basal impression, but less so than the infrabasals. However, the steepest longitudinal slopes of the basals are in their proximal portions; the convexity in the midregion is slight, but the upward (distal) slope is fairly steep. These plates are strongly concave from side to side proximally. They continue to be concave from side to side, although much more gently, to their midregion and even beyond their proximal contact with the radials along the lateral wall of the cup. Beyond the steep wall of the basal impression the basal sutures are slightly impressed. The distal margins of the basals are gently curved. At all angles where the basals and radials meet, these plates are inflexed to form the characteristic *Endelocrinus* pits.

The ornamentation of the basals is of two types. One type consists of closely spaced rounded granules that cover the entire plate except for the steep wall of the basal impression. The other is in the form of coarse nodes that are confined to the distal part of each plate. The most proximal of these nodes are paired and shared by adjacent basals near the distal termination of each interbasal suture. The basal plane is tangent to the tips of these paired nodes.

The radials are a little more than two-thirds wider than long. They show slight convexity along their length, although each is rather abruptly incurved near the summit, forming a distinct forefacet. The transverse curvature is moderate and most pronounced about midheight. The ornamentation comprises nodes and granules similar to those on the basals. The forefacet is free of nodes, but there is a node at the lateral termination of each radial at the summit. Otherwise the radials bear no nodes closely adjacent to the interrarial sutures.

The radial facets are relatively shallow. The outer ligament area is short and is denticulate in the region external to the slitlike ligament pit which occupies most of its extent. The transverse ridge extends essentially to the full width of the facet; it is fairly well defined and denticulate. The inner ligament fossae are rather deep and extend almost parallel to the transverse ridge to points nearly opposite the terminations of the outer ligament area. The

oblique ridges are strong and denticulate. The intermuscular notch is quite broad and there appear to be indications of muscle areas flanking the intermuscular furrow. The lateral ridges face outward, but are relatively low. The adsutural slopes are gentle and the adsutural platforms extensive.

Anal X has been displaced; its distal end lies in the body cavity and the entire plate has shifted inward between the posterior radials. Proximally, anal X rested on the truncated tip of the posterior basal, and along with the basal and radials was inflexed to form a small pit on each side at the angles where it met those plates. For most of its height anal X is slightly concave from side to side. It bears a single distal facet for articulation with a second anal plate.

A single axillary first primibrach, that of the E ray, remains in place. It is more than twice as wide as long, and bears a short but distinct spine. In addition to granulose ornamentation similar to that of the dorsal cup, this plate bears a node on each lateral shoulder, below and flanking the spine.

The distal articular surface of the primibrach is divided into right and left facets by a prominent, partly denticulate ridge. The right facet is fully exposed. It shows an outer ligament area that is relatively longer and much less compressed than the outer ligament areas of the radials. This ligament area is denticulate. The external ligament pit is slightly elongate but not slitlike as in the radials. It does not occur at midlength of the ligament area, but is somewhat nearer the termination of the area in the vicinity of the ridge that separates the facets. A strong denticulate transverse crest is present, together with well-defined ligament fossae. Although most of the articulation appears to have been of the ligamentary type, structures on the inner side of the ridge that separates the facets strongly suggest muscle scars.

The first two secundibrachs of the left arm of the E ray are also present. The first secundibrach has been displaced outward, carrying the second with it. Both of these plates show granulose ornamentation. The first secundibrach bears a nodose swelling on the right side. The second secundibrach displays a large node or blunt spine in this region.

The first secundibrach is quadrangular and about three times as wide as long. Because of the position of the plate I have not been

able to determine whether it bore a pinnule and interlocked with adjacent plates, although presumably it did.

The second secundibrach is quite low and elongate from side to side in external view. Because its lateral terminations are both angular, it is not a typical cuneate plate. Laterally, the plate shows structures for interlocking with plates of adjacent arms. These are especially evident as bulbous swellings on the left (pinnular) side. A pinnule socket is present on the internal side. The distal articular facet bears a prominent crenulated outer ligament area, traces of an outer ligament pit, and a transverse crest. The inner ligament area is more extensive on the left (pinnular) side, and extends inward and laterally in that region, rising up to a rounded prominence well above the rest of the articular surface. Along the outer border of this left side, but internal to the transverse crest, are additional crenulations.

The intermuscular notch of this second secundibrach is sharply angular and the intermuscular furrow originates near the transverse crest. The flexor muscle scar of the left (pinnular) side originates along the internal reaches of the intermuscular furrow and extends as a channel bordering the pinnular side of the intermuscular notch for about half the length of that side of the notch. The channel expands widely toward its termination.

The flexor muscle scar of the right (antipinnular) side of this second secundibrach is separated from the muscle scar of the pinnular side by the intermuscular furrow, and runs parallel to the latter to a point a little beyond the exit of the furrow. It is deeper than the scar on the pinnular side, but much less elongate.

To the right of the antipinnular muscle scar the articular surface is rounded, elevated, and bears crenulations suggestive of ligament attachment areas. From that place to the transverse ridge the antipinnular articular surface is concave and slopes gently laterad.

Linear measurements of the holotype specimen, in millimeters, are shown in the following tabulation:

Height of dorsal cup	7.5
Width of dorsal cup	21.0
Ratio of height to width	0.36
Height of basal impression	4.2
Width of basal impression	8.8
Length of basal (raB)	7.1
Width of basal (raB)	8.3
Length of radial (laR)	6.5

Width of radial (laR) -----	11.2
Length of suture between basals -----	5.4
Length of suture between radials -----	3.4
Length of anal X -----	4.4
Width of anal X -----	3.6
Length of first primibrach (E ray) -----	5.0
Width of first primibrach (E ray) -----	11.6
Length of first secundibrach (E ray) -----	2.5
Width of first secundibrach (E ray) -----	7.5
Length of second secundibrach (E ray) -----	1.8
Width of second secundibrach (E ray) -----	5.8

Remarks: In ornamentation, *Endelocrinus undulatus* (Strimple, 1961) bears resemblance to this species, although the nodes are apparently less prominent. In addition, *Endelocrinus undulatus* is a smaller species, the dorsal cup is relatively higher, the basal impression is wider, the primibrachs do not bear spines and both primibrachs and secundibrachs have greater height.

From the standpoint of size, *Endelocrinus pennsylvanicus* appears to be the largest Pennsylvanian representative of the genus.

Knapp (1969) would restrict *Endelocrinus* to two species, *Endelocrinus fayettensis* (Worthen) and *Endelocrinus bifidus* Moore and Plummer, characterized by gently downflaring infrabasals. He includes *Endelocrinus texanus* (Weller) in his proposed genus *Metarrectocrinus* for the same reason. He emends Strimple's genus *Tholiocrinus*, which as originally proposed, was considered synonymous with *Endelocrinus* by Burke (1966) and Webster and Lane (1967) because it was based solely on ornamentation, a feature insufficient for generic distinction. As emended by Knapp, the sole basis for distinction between *Endelocrinus* and *Tholiocrinus* would be steeply downflaring infrabasals, which he assumes to characterize *Tholiocrinus*.

Dorsal cups of *Endelocrinus* are distinguished by the characteristic pits at the angles where the radials and the basals meet, and usually by convexity or even bulbosity of these plates of the cup. These salient generic characters are shown in common by *Endelocrinus fayettensis*, *Endelocrinus texanus*, *Endelocrinus bifidus*, and the various species of *Endelocrinus* which Knapp would lump together under *Tholiocrinus*. There is no evidence that the degree of downflaring of the infrabasals modifies the dorsal cups of these species to the extent that the generic characters cited above are not evident. For this reason I regard *Tholiocrinus* as emended by Knapp to be a synonym of *Endelocrinus*.

Genus **PARADELOCRINUS** Moore and Plummer, 1938

PARADELOCRINUS DECORATUS sp. nov.

Fig. 3

Diagnosis: A relatively large species of *Paradelocrinus* (width of dorsal cup 25.7 mm); form ratio .37; cup pentagonal in ventral view; basal impression deep and about half as wide as the cup; basal plates concave from side to side at basal plane; basals and radials ornamented with fine ridges and prominent nodes.

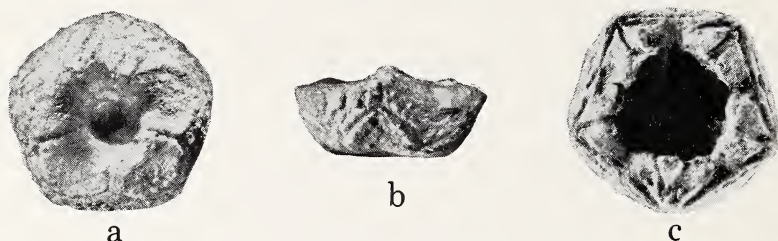


Fig. 3. *Paradelocrinus decoratus* sp. nov. Holotype, Cleveland Museum 3914, from the Ames Limestone, Conemaugh Group, Brooke County, West Virginia. a, dorsal view; b, posterior view; c, ventral view, $\times 1$.

Holotype: Cleveland Museum of Natural History 3914, a dorsal cup complete except for the infrabasal circlet.

Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Excavation (Tunnel Road Cut) for West Virginia Route 67 (lat. $40^{\circ} 14' 24''$ N., long. $80^{\circ} 35' 53''$ W.) near McKinleyville, Brooke County, West Virginia.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

Description: The dorsal cup is low, truncate bowl-shaped and nearly three times wider than high. It is subpentagonal in dorsal view and pentagonal in ventral view. The basal impression occupies about half the diameter of the cup. The impression was evidently quite deep, but the infrabasal circlet, which represented about one-seventh of the cup diameter, is missing and the full height of the impression cannot be determined.

The basal plates comprise most of the base of the cup; their distal tips extend for more than half the height of the radials. All

of the basals, including the posterior basal, which is longer than the others, are pentagonal in outline. These plates curve rather strongly upward into the basal impression proximally; distally, beyond the basal plane, they again curve upward, but more gently. Each basal plate is also a little concave from side to side. The basal plane in consequence, is tangent to points along the basal sutures, but a gentle concavity characterizes these plates distally, well above the basal plane. The distal margins of the basals are rounded to the tips, rather than angular.

Each of the radial plates is pentagonal in outline and nearly twice as wide as high. In keeping with the longer posterior basal plate, the suture between the two posterior radials is shorter than the other interrarial sutures. Proximally the radials slope outward and upward with little convexity, retaining the distal slope of the basals. Toward the summit of the cup the radials become a little more convex from side to side, and more convex along the length, just below the outer ligament area.

The articular facets of the radials are of medium depth. The outer ligament area is narrow and elongate, with a slitlike outer ligament pit. The transverse crest extends to the lateral extremities of the facet and is denticulate. In the inner ligament area the lateral furrows are elongate and rather narrow and the oblique ridges are denticulate. The adsutural slopes are abrupt and the adsutural platforms wide. The lateral ridges slope outward fairly strongly. The intermuscular notch is broad, leading into a short intermuscular furrow. A broad, low, concave region, representing the two muscle areas, is bordered by the notch and divided by the furrow.

Anal X is entirely shut off from the outer side of the cup by the posterior radials, which share a CD interrarial suture on that side. At the summit of the cup the left lateral corner of the C radial is slightly elevated and bent inward. At the termination of this prolongation of the radial corner, anal X fits between the lateral ridges of the adjacent posterior radials. In ventral view the plate is triangular in outline; it widens as it approaches the body cavity and rises above the inner articular surfaces of the radials. Its ventral surface bears a facet for articulation with a second anal plate.

The ornamentation is of two kinds, the most prominent consisting of nodes on the radials and the basals. On the radials the nodes are arranged in three rows. The proximal two rows tend to parallel

the sutures between the radials and the basals. The distal row is somewhat transverse and the nodes are larger than those of the proximal rows. There is also a row of nodes on each basal, which borders the sutures between the radials and the basals, and nodose swellings border the interbasal sutures distally. Irregular nodes are also distributed over the portions of the basals that rise above the basal plane. The sutures are not impressed, but where nodes border the sutures they appear to be.

A second, finer kind of ornamentation comprises wrinkles or ridges on the basals and the radials. These ridges also extend across the nodes, where in general they show an arrangement at right angles to the sutures. The wrinkled ornamentation persists part way into the basal impression.

Linear measurements of the holotype, in millimeters, are as follows:

Height of dorsal cup	9.5
Width of dorsal cup	25.7
Ratio of height to width	0.37
Width of basal impression	10.8
Length of basal (raB)	9.5
Width of basal (raB)	9.9
Length of radial (aR)	7.6
Width of radial (aR)	15.5
Length of suture between basals	7.1
Length of suture between radials	4.3
"Length" of anal X	5.3
Width of anal X	3.3

Remarks: In comparison with the genotype species, *Paradelocrinus aequabilis* Moore and Plummer, 1938, *Paradelocrinus decoratus* appears to be a fairly typical representative of the genus. It is, of course, a much larger species than *Paradelocrinus aequabilis*, the cup is higher, the basals are more prominent, and the cup is ornamented. Nevertheless, in the outward flare of the cup walls, deep basal impression and appearance of anal X, it is closer to *Paradelocrinus aequabilis* than many other forms that have been referred to *Paradelocrinus*.

There are some resemblances between *Paradelocrinus decoratus* and *Paradelocrinus planus* (White, 1880) in cup height, depth of basal impression, and size of basal circlet, but the cup of *Paradelocrinus decoratus* is larger, more pentagonal, and ornamented rather than smooth.

In ventral view, *Paradelocrinus iolaensis* Strimple, 1949, is reminiscent of *Paradelocrinus decoratus* in its pentagonal outline and appearance of anal X. The basal plates of *Paradelocrinus iolaensis* are concave from side to side in the vicinity of the basal plane, but more concave than those of *Paradelocrinus decoratus*. The dorsal cup of Strimple's species is also smaller, of lesser height, more pentagonal in dorsal view, and unornamented.

The Atokan species described by Knapp (1969) as *Atokacrinus obscurus* is likewise similar to *Paradelocrinus decoratus*, although the dorsal cup is not as high. The dorsal cup of the Knapp type is worn, and may have borne ornamentation, but the flattened depressed areas that bound the sutures do not characterize the cup of *Paradelocrinus decoratus*. Like those of *Paradelocrinus decoratus*, the basals of Knapp's species are concave from side to side at the basal plane.

In proposing *Atokacrinus* as a new genus, Knapp gives for a diagnosis "Basal concavity deep, infrabasals steeply downflared." Knapp has also proposed a new genus, *Sublobalocrinus*, to include *Paradelocrinus iolaensis* and *Paradelocrinus planus*, based on the following diagnosis: "Basal concavity narrow and deep; infrabasals steeply downflaring, basals transversely concave; arms unknown."

Like *Paradelocrinus aequabilis* and *Paradelocrinus decoratus*, the species comprising Knapp's proposed new genera are fairly conservative forms, which, except for the characteristic curvature of the cup in lateral view and absence of anal X from the outer side of the cup, strongly resemble the dorsal cups of various species of *Delocrinus*. For such forms, Knapp's generic characters might have specific, but not generic weight, and I regard *Sublobalocrinus* and *Atokacrinus* as synonyms under *Paradelocrinus*.

DISCUSSION

This article was essentially completed before the appearance of Knapp's (1969) paper dealing with his proposed new order Declinida. As a consequence some revision was necessary in order to deal with new taxa introduced by Knapp and various taxonomic changes which he advocates. I feel obligated to summarize certain of my views concerning the content of Knapp's paper, however, since I fail

to find justification for the establishment of the Declinida as a new order.

Knapp (ibid. p. 343) contends that in the Inadunata, downflaring infrabasals cannot have evolved from infrabasals that were originally upflaring, and states: "With the infrabasals established as a stable element in the dorsal cups of crinoids having anal X and radial plates, the stage was set for the origin of a basal concavity having steeply downflaring infrabasals. The origin of steeply downflaring plates can be envisioned by reference to the position at which the infrabasal plates appear in the early growth stages of Recent crinoids, that is, deep within the basal circlet and steeply flaring. Rather than moving down from within the basal circlet as in Recent crinoids and presumably inadunates incorporating upflaring infrabasals, the infrabasal plates remained deep within the basal circlet and a basal concavity was created in fossil inadunates. As in fossil inadunates possessing upflaring infrabasal plates, evolution proceeded from steeply downflaring infrabasals to horizontal infrabasals and a flat base."

Knapp's theory that the basal concavity and downflaring infrabasals originated in the larval stage is a novel one, to say the least. Such major evolutionary changes are usually developed in gradual stages over long periods of time, and are traceable in adult forms. However, it may be questioned whether the larvae of modern crinoids, which share the extreme specialization of the adult forms, can be taken as indicators of an evolutionary sequence such as Knapp outlines.

In *Antedon adriatica* Clark (1921, p. 414), in a summary of Seeliger (1893) reports that at the earliest larval stage at which the infrabasals are found, they are anterior to the basals. On the other hand, Mortensen (1920, p. 26, pl. 12, fig. 3) finds the first detected infrabasal plate of *Compsometra serrata* lying within the basal circlet. But it is not until later stages, when the infrabasals are surrounded by the faster growing basal plates that they can be described as "deep within the basal circlet and steeply flaring." I fail to find evidence to support Knapp's view that the basal concavity of inadunates arose as a spontaneous development in the larval stage.

Knapp (1969, p. 351) stipulates that for inclusion in the Declinida the crinoid must possess what he terms a "structural" basal

concavity—the infrabasals must flare downward. I gather from this that if the walls of the concavity were composed of the basals and were topped by a horizontal infrabasal circlet, an inadunate showing such a concavity would be excluded from the Declinida. However, it is evident that if the one type of concavity could have arisen in the larval stage, the other could have also.

It appears far more likely that the stages in evolution from up-flaring to flat and finally to downflaring infrabasals illustrated by Moore, Lalicker and Fischer (1952, p. 624) represent the true course of change in attitude of these plates, rather than that suggested by Knapp. The latter writer quite apparently holds no brief for the derivation of downflaring from flat infrabasals. Attributing the decrease in steepness and flare and eventual “horizontality” of the radial and basal plates of *Antedon* to differential accretion of calcite during growth, Knapp (1969, p. 343) contends that these plates cannot change their horizontal attitude, once it has been attained, by accretion of calcite at their lateral margins. At this “horizontal” stage the plates are probably joined by zygositystosial articulations, which, as Van Sant (1964, p. 39) states, are mostly immovable.

Now it is true that such articulations could prevent horizontal infrabasal plates from progressing to a downflaring attitude, and indeed zygositystosial articulations appear to characterize the adjacent sides of flat infrabasal plates of various Upper Carboniferous inadunates. However, I have observed specimens of *Polusocrinus*, *Aesiocrinus*, *Parulocrinus* and *Ethelocrinus* in which individual plates are separated from others in the circlet or shifted from sutural position in such a manner as to suggest very slight calcareous deposits and the probability that at early stages of growth they were bound together by connective tissue only.

It seems reasonable to me that a similar very loose sutural union bound together the infrabasal plates of inadunates during the evolutionary transition from upflared to downflared plates that produced the basal concavity. Probably in early stages of growth the circlet remained flat and was supported at the center by the stem, but with the increase in weight of the expanding dorsal cup the infrabasals sagged downward, extending below the top of the stem peripherally, thus giving rise to the basal concavity. Calcite deposition may have been arrested up to this point; the height of the concavity in that case probably depended on (1) the rate of renewed calcite deposition leading to zygositystosial articulation and

(2) the rate of upgrowth, if any, of the proximal portions of the basals.

Upgrowing basals probably influenced the angle of flare of the downflaring infrabasals before zygosynostosal articulations developed. Apparently synostosal articulation was not unusual between the basals and infrabasals of some Upper Carboniferous inadunates. In some species of *Delocrinus*, where such articulations occur, a slender flange at the proximal tip of each basal inserts into a short notch in the infrabasal circlet, preventing the closure of the infrabasal suture at that place. This indicates that prior to the time that the infrabasals were united by close suture they were separated, to some extent at least, by the basal tips. It would appear that in such specimens, if there is any possibility that the infrabasals are not yet joined by close sutures, it would be unwise to assume that the angle of flare of the infrabasals was stabilized and representative of the particular species involved.

If the infrabasal circlet had remained flat, and was bound to the proximal portions of the upcurving basals by loose suture, the continued growth of the basals would have resulted in their forming the walls of the basal concavity, with the infrabasal circlet roofing the concavity. This is the type of basal concavity found in *Plummericrinus*. Since from a mechanical standpoint such a concavity seems to have served the same purpose as one with downflaring infrabasals, I fail to see why Knapp considers the distinction between the two of major taxonomic importance.

Obviously I do not agree with Knapp that evolution of the taxa he includes in the Declinida proceeded from downflaring infrabasals to horizontal infrabasals and a flat base. Of course it is possible, because all stages are represented in the sequence from flat base to steeply downflaring infrabasals, to juggle various species of Upper Carboniferous inadunates into groups arranged in chronological order supposedly illustrating the reverse of that sequence. But many of these species are based on single specimens, and few are represented by an adequate number of individuals to determine extent of variation within a species, or to permit ontogenetic studies. Such being the case, to assume constancy in the angle of flare of the infrabasals in such species is not justified.

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A NEW ANTHRACOSAURIAN LABYRINTHODONT,
PROTEROGYRINUS SCHEELEI,
FROM THE LOWER CARBONIFEROUS

ALFRED SHERWOOD ROMER

Museum of Comparative Zoology, Harvard University

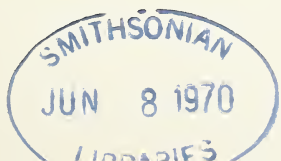
ABSTRACT

Incomplete remains of the skull and skeleton of an anthracosaurian labyrinthodont from the basal part of the Mauch Chunk Group of the Mississippian of Greer, West Virginia, are described as *Proterogyrinus scheelei*, gen. et sp. nov. and made the type of a new family Proterogyrinidae. The type resembles the Embolomeri in most regards but is more primitive in that both intercentra and pleurocentra are in the form of dorsally incomplete rings.

INTRODUCTION

As noted in a previous publication in this series (Romer, 1969), almost nothing has been known of labyrinthodont amphibians in the earlier, Mississippian, portion of the Carboniferous. This lacuna is in process of being filled in considerable measure by specimens from the Greer quarry in West Virginia. In my previous paper I noted the history and stratigraphy of the locality. In that paper I described the skull and partial skeleton of a rhachitome from Greer; specimens of an anthracosaur and a second rhachitome are in process of description by Dr. Nicholas Hotton III; several further Greer specimens are in process of study and collection. It is to be hoped that before the possibilities of the Greer quarry are exhausted we may attain a broad representation of the labyrinthodont fauna of the Lower Carboniferous of North America.

Science is indebted to Mr. John J. Burke and Mr. William E. Moran and, more recently, to Mr. William Hlavin for their success-



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ful exploration of the Greer site, to the Greer Limestone Company, owners of the property, for their cooperation, and to Mr. William E. Scheele, Director of the Cleveland Museum of Natural History, for his promotion of the work.

In the present paper is described an anthracosaur differing from that under description by Dr. Hotton. The specimen is fragmentary in nature, but is of interest, particularly, as showing a hitherto unknown type of anthracosaurian vertebral structure.

SYSTEMATIC PALEONTOLOGY

Family PROTEROGYRINIDAE fam. nov.

Diagnosis: Anthracosaurian labyrinthodonts, resembling typical embolomeres in most regards, but with both intercentra and pleurocentra in the form of incomplete rings, open dorsally. Type genus *Proterogyrinus*.

Genus *Proterogyrinus*¹ gen. nov.

*Proterogyrinus scheelei*² sp. nov.

Figs. 1-8

Diagnosis for genus and species: Structure, so far as known, similar in most regards to such an embolomere as *Archeria*. Snout moderately elongate; length of frontal and nasal combined nearly twice as long as parietal and postparietal. Skull roof lightly sculptured with small shallow pits and short grooves.

Holotype: Cleveland Museum of Natural History 10950.

Occurrence: Bickett Shale of the Bluefield Formation, Mauch Chunk Group, Mississippian.

Locality: Greer, Monongalia County, West Virginia, on Deckers Creek, about 6½ miles southeast of Morgantown.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

¹ The generic name continues the series of anthracosaurian names based on "gyrinus" by Watson, and suggests the relative antiquity of the present form.

² The specific name is in honor of Director William E. Scheele, who has enthusiastically promoted the search for Greer amphibians.

DESCRIPTION

Cranial remains: Two large slabs show disarticulated and scattered postcranial remains; a smaller block contains incomplete remains of cranial structures (as well as several anterior vertebrae) (Figs. 1-2).

Best preserved of skull materials are the dorsal series of roofing bones, from nasals back to postparietals and tabulars. These are preserved almost intact except for some disruption of the right side of the table posteriorly. This type of preservation of the skull roof is common in anthracosaurs, due principally to the loose connection of skull table and cheek in typical members of this group, and aided anteriorly by the apparently sharp drop of the sides of the snout from the frontals and nasals. For example, in the Harvard collection of *Archeria* materials from the Geraldine bonebed of the Texas Permian, no less than five specimens show a complete or nearly complete series of dorsal roofing elements broken off from the elements of the side of the skull. The skull roof is but lightly sculptured; near centers of ossification there are groups of small, shallow pits; farther out one finds a series of short and shallow radiating grooves. Of lateral line grooves, only faint and uncertain traces are to be seen.

The skull table structures are comparable to those of embolomeres. Slender tabular "horns" are present, although broken off. In the lateral series of table elements, the tabulars are somewhat larger than typical, and in consequence the two temporal elements are somewhat reduced in size. The suture between intertemporal and supratemporal is obscure, but apparently the former element is of small size. The parietal does not expand as much postero-laterally as is usually the case.

Facial length is variable in anthracosaurians, but snout elongation is common in embolomeres. If we assume that the joint length of parietals plus postparietals is relatively constant, we find that, for example, the length of nasals and frontals together is about 180 percent of this figure in *Palaeogyrinus*, 260 percent or so in members of the *Pteroplax-Eogyrinus* group, 300 percent and upward in *Archeria*. *Proterogyrinus* is relatively short faced, with nasal and frontal about twice the length of the posterior table elements.

Apart from the dorsal roofing elements, skull remains are few and generally scattered. Fragments of both prefrontals and of the



Fig. 1. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. The block exhibiting cranial materials, $\times \frac{3}{4}$.

left postorbital are seen adjacent to the dorsal series. Far to the right of the skull table is a roughly triangular mass of bone which may represent the right cheek area of squamosal and quadratojugal. Several other pieces of bone lying to the right of the skull roof may be part of the dermal elements of the right side of the face, but I have not attempted to identify them.

To the right is found a crushed but nearly complete right pterygoid, seen from the inner or lower surface; in its extent it is comparable to that of *Palaeogyrinus* as figured by Watson (1926) and by Panchen (1964). The thickened portion of the epipterygoid supporting the anteroventral surface of the basipterygoid process is evident, but the more dorsal region of the socket for the process is not clear. A bar of bone rising straight upward from this area is presumably an imperfect columella cranii; whether further remains

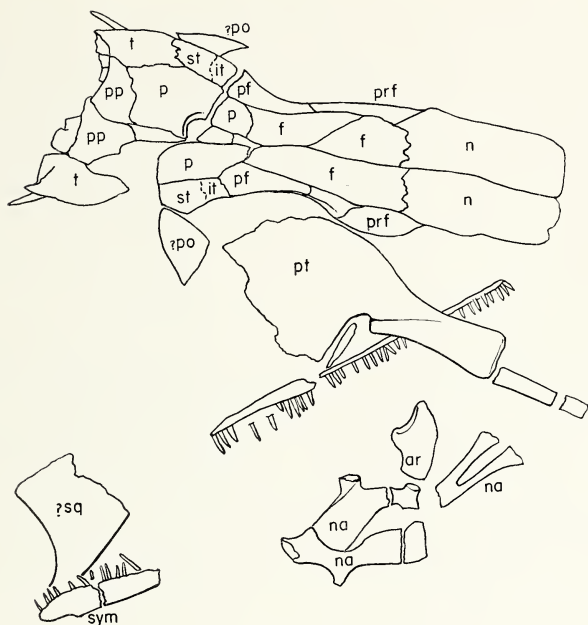


Fig. 2. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. To show, in outline, identified elements present on the block shown in figure 1, $\times \frac{3}{4}$: ar, articular region of right lower jaw; f, frontal; it, intertemporal; n, nasal; na, neural arch; p, parietal; pf, postfrontal; po, postorbital; pp, postparietal; prf, prefrontal; pt, pterygoid; sq, squamosal; st, supratemporal; sym, symphyseal region of right lower jaw; t, tabular.

of the epipterygoid are present, concealed beneath the pterygoid, cannot be determined.

A bar of bone bearing about 40 teeth (plus a few empty alveoli) is seen to the right of the series of dorsal elements.¹ The tooth row is of length appropriate to its being considered nearly a full dentition for a maxilla or dentary of the present specimen. Most of the teeth are about 3 mm long, subcircular in section, about $\frac{3}{4}$ mm in diameter and closely spaced. In some cases the basal section of the tooth can be seen to be grooved in labyrinthine fashion. The tips are blunt and when well preserved appear to be bevelled and tilted slightly toward that end of the bar which lies anteriorly on the slab.

¹ A section of this series running beneath the pterygoid has been developed since the photograph of figure 1 was taken.

The nature of this tooth-bearing element is somewhat puzzling. At first sight one would assume that it is the right maxilla, little displaced. But there is a distinct longitudinal shelf the length of the bone, superficial to the teeth as they lie on the bone. We are, hence, looking at the inner surface of the bone. But if the bone is a maxilla, it must be either the left element strongly displaced, or the right maxilla rotated nearly 180° . Suggesting the latter interpretation is the fact that the teeth which lie most anteriorly are smaller than most of the series, and hence may pertain to the posterior end of the tooth series.

To add complexity to the situation, there are present, further to the right in the slab and not far from the "front" end of the tooth-bearing element, the articular end of a right lower jaw and, far to the rear, the symphysial end of a right jaw. It is tempting to consider that the major structure we are dealing with is a dentary, rather than a maxilla. However, to make it a right dentary requires not only that the smaller teeth be considered anterior, but necessitates such a complex post-mortem juggling of parts that it seems

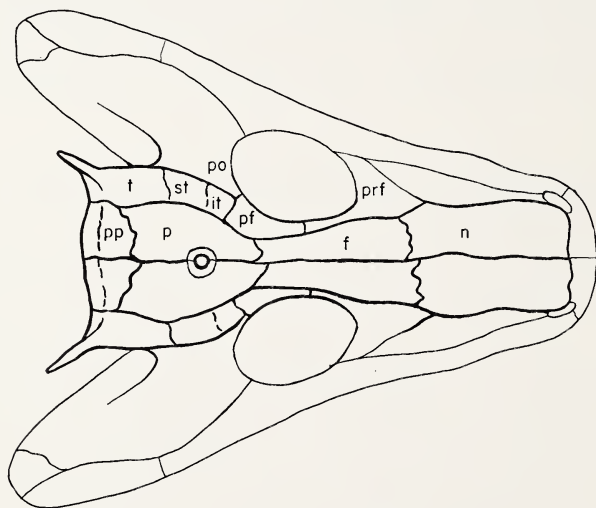


Fig. 3. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. Attempted restoration of skull in dorsal view. Heavy lines indicate parts preserved in the specimen; light lines, lateral portions of skull restored in embolomere pattern. Abbreviations as in fig. 2, $\times \frac{3}{4}$.

better to keep to the assumption that we are dealing with a displaced right maxilla.

Assuming normal proportions and arrangement of the dermal roofing elements as found in other anthracosaurs, one can tentatively restore the appearance of the skull as seen in dorsal view (fig. 3). Material is obviously insufficient for an attempt at a lateral or ventral reconstruction.

POSTCRANIAL SKELETON

Axial skeleton: From the small block containing the remains of the skull, disarticulated postcranial materials are sparsely spread over two slabs extending for about 70 cm. Except for a partial *Megalichthys* jaw near the far end of the slabs, all material visible is of a sort which could have been derived, and presumably did derive, from a single animal. All identifiable materials are appropriate to a form with body and limb proportions similar to those of the embolomere *Archeria*, and in various points the structure of limb and girdle remains are comparable to those of typical embolomeres. Despite their disarticulated and scattered nature, the various preserved fragments indicate that the individual had not completely "disintegrated" before burial; for example, the remains of the front leg are close to the skull block, remains of the pelvic girdle are toward the far end of the pair of slabs.

There are sparse scattered remains of the vertebral column. Several neural arches, presumably from the cervical region, are present on the skull slab. About a dozen arches from the trunk region can be seen; on the larger slabs most are crushed or incomplete, and surface detail is generally obscure. However, the general structure can be made out (fig. 4 D,E). It is of a normal anthracosaurian type. The neural spine is moderately tall, thin from side to side, and broad anteroposteriorly. Below, the arch expands anteriorly and posteriorly to the zygapophyses; further ventrally and somewhat anteriorly the arch extends downward to, presumably, afford tubercular attachment for the rib externally, and internally shows a flat surface for "central" attachment.

Separated from the arches there are found some eight "central" elements (fig. 5). They are thin hoops of bone, forming the greater part of a circle but incomplete at one point, presumably dorsally

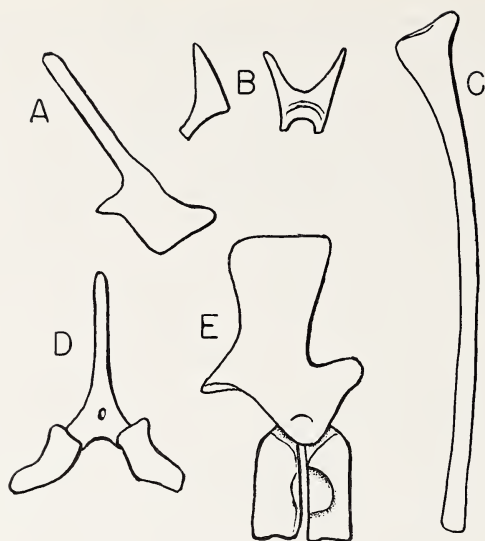


Fig. 4. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. A, a caudal neural arch, seen from the right side. B, a caudal intercentrum and haemal arch base, seen from the side at the left, anteroventrally at the right. C, a rib; position in column indeterminate. D, a dorsal neural arch in anterior view. E, a dorsal neural arch in side view; central elements are restored in probable position, $\times 3/2$.

in the articulated position. The upper edges are bevelled, obviously for neural arch articulation. Most of these central elements are poorly preserved, but several, when seen in side view, have nearly straight edges, with little indication of structural features except for a slight indentation seen in two cases part way down the presumed anterior border. One element, however, is of a different nature, and a second element appears to resemble it. Here, part way down each side, there is a pronounced development of a semi-circular area of articulation for a rib capitulum along the presumed



Fig. 5. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. "Central" elements of the trunk. A, presumed intercentrum from the right side and posteriorly. B, presumed pleurocentrum from the right side and posteriorly, $\times 3/2$.

posterior margin of the outer surface. It seems probable that we have in these ring-shaped structures both pleurocentra and intercentra, those with the pronounced articular area being intercentra, the others pleurocentra. I have ventured to restore a vertebra in side view (fig. 4 E). This restoration should, of course, be considered as tentative only, because of the sparsity and disarticulated condition of the material. As seen in side view, the vertebra appears closely comparable to that of a typical embolomere. It must be remembered, however, that the central elements are merely thin shells, in strong contrast to the centra of such a typical embolomere as *Archeria* and, further, that the "central" rings, as preserved, are incomplete dorsally. It is not impossible that in a more mature specimen of *Proterogyrinus* this dorsal gap might have been closed; but it is highly improbable that, even so, the elements would have been closely comparable to those of typical embolomeres, in which ossification is as complete dorsally as around the rest of the circle of the centrum. Of the caudal region I have been able to identify a single neural arch, of relatively small size and with a slender backwardly-slanting spine (fig. 4 A). Adjacent to one of the ischia there are badly preserved remains of the central elements of a fraction of the tail region. There are here several intercentral elements, from which the haemal spines have broken off (fig. 4 B). The associated intercentra appear, as far as preserved, to be wedge-shaped, as seen in side view, tapering to a point dorsally. A crushed and poorly preserved element nearby appears to be a completely circular structure. Possibly pleurocentral development may have been more advanced in the caudal region than in the trunk.

In the neighborhood of the front limb are remains of two clusters of ribs which presumably come from the anterior part of the column. The rib heads are not visible. They are circular in section, and show none of the flattening seen in various temnospondyls, and there is no evidence of expansion of the shaft (except for a slight distal expansion seen in one case). A few further ribs are seen farther posteriorly in the block; one is shown in figure 4 C.

There are a number of belly scales, poorly preserved, scattered over the slabs.

Appendicular skeleton: There are no identifiable remains of the shoulder girdle. Of the left pectoral limb there is only an imperfectly preserved humerus. Of the right leg, however, humerus,

radius and ulna are present close together in a semi-articulated condition (fig. 6 A).

The humerus, which measures 30 mm in overall length, is closely comparable to that of the embolomeroous *Archeria* in general build. The bone is less completely ossified than in most specimens

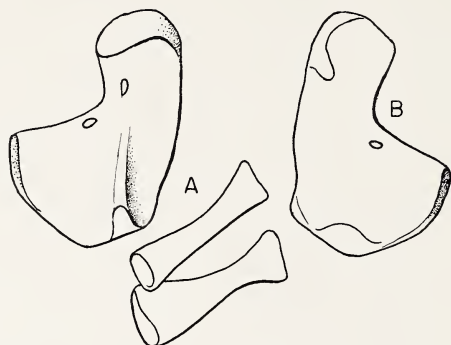


Fig. 6. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. A, right humerus; radius and ulna in position as found. The humerus is seen from the dorsal surface. B, the same humerus in ventral view, $\times 1$.

of that genus, so that the "unfinished" proximal surface extends anteroventrally to include the region of the deltopectoral crest, and distally the ectepicondyle, presumably projecting in an adult, is unossified. As in *Archeria*, the entepicondyle is a very large subquadrate structure, bearing, as is proper for anthracosaurians, an entepicondylar foramen near its proximal inner corner. As in embolomeres, a highly developed flange of bone extends from the region of the deltopectoral crest distally, without interruption, along the anterior edge of the bone, to the ectepicondylar region.

Radius and ulna are seen from the dorsal (extensor) aspect; the former is 18 mm in length, the latter 20 mm. It is obvious that ossification was far from complete, for in the ulna there is no olecranon and not even any trace of the articular surface for the humerus.

Situated some 60 mm from the major limb bones is a series of disarticulated foot elements which are not improbably part of the right front foot (fig. 7). Presumably, the four stouter elements are metacarpals.

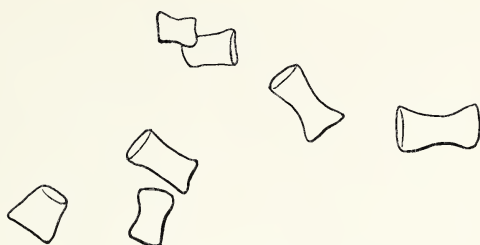


Fig. 7. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. Scattered foot bones found near right leg elements, $\times 1$.

Of the pelvic girdle (fig. 8) the left ilium is present, and seen from the inner surface, and there are both ischia, the right seen from the inner surface, the left from the outer side. The greatest length of the ilium, from the pubic articulation to the tip of the posterior prong is 54 mm. The right and left ischia are, respectively, 33 and 32 mm in greatest length. The ilium is closely comparable

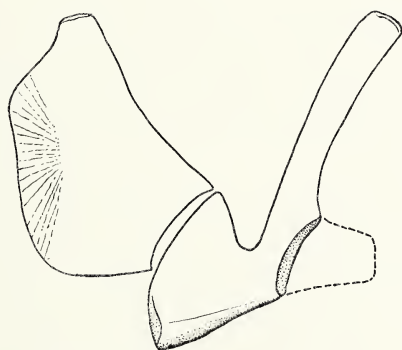


Fig. 8. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. Left ilium and ischium, seen from inner surface. The ischium is that of the right side, reversed, $\times 1$.

to that of *Archeria*. There obviously was a dorsal blade, for sacral connection, but this is broken off. The posterior prong is as elongate as that of *Archeria*. Since the element is seen from the inner side, nothing can be said of acetabular structure. The base of the bone presents a much thickened articular surface for pubis and ischium, the pubic area being especially thick. Anteriorly there is a well

developed triangular buttress leading down to the region of pubic articulation. This area faces nearly directly anteriorly, in contrast to its somewhat more medial slant in *Archeria*.

The ischium, again, is comparable in proportions and build to that of *Archeria*. The outer surface shows a gentle indentation for the acetabular border. As in early tetrapods generally the upper margin of the posterior projection of the bone is somewhat thickened. The area of the ischiadic symphysis is striated in a fashion seen in various early tetrapods.

No pubis is present in the material. Whether this is due to chance, or whether (particularly taking into account the immaturity of the specimen) the pubes were unossified, is, of course, uncertain.

Except for three phalanges or metapodials no identifiable remains of the hind leg are present.

DISCUSSION

Despite the fact that the remains are incomplete, the nature of *Proterogyrinus* seems clear as regards most features. The form is clearly an anthracosaurian; further, in most regards it is in close agreement with the Embolomeri of the Pennsylvanian and early Permian. Such portions of the skull as are preserved show a close approach to the structure seen in such representative Upper Carboniferous forms as *Pteroplax*, *Eogyrinus*, and *Palaeogyrinus* of the English Coal Measures (Watson, 1926; Panchen, 1964), *Neoptero-plax* of the American Pennsylvanian (Romer, 1963), and, except in a lesser elongation of the snout, *Archeria* of the early Permian.¹ Even in the nature of the marginal teeth—small, numerous, closely crowded and with “chisel-like” tips—there is a clear comparison with embolomeres far removed in time, such as *Archeria* of the Permian. The humerus (except in the fact that ossification is less advanced) is closely comparable to that of such an embolomere as *Archeria*. The pelvis, too, is of a nature comparable to that of known embolomeres.

¹ Figures of the roof of the *Archeria* skull (as “*Cricotus*”) have been given by Cope (1884), by Cope and Matthew (1915), and by Broom (1913). I hope to give a more complete description of *Archeria* cranial anatomy in the near future.

Were it not for the structure of the central region of the vertebrae, *Proterogyrinus* could well be considered a proper member of the Embolomeri, hardly to be distinguished on a family basis from various other members of that group. The central elements, however, give one pause. All previously known embolomeres in which vertebral material is present show both intercentra and pleurocentra as complete rings, as well ossified dorsally as laterally and ventrally, and with a thickness of ossification that reduces the opening for the notochord to a fairly modest diameter. In the present specimen the walls are relatively thin; most especially, both intercentrum and centrum are incomplete dorsally, with a broad gap in the region which in life lay below the neural canal. It must be kept in mind that the present specimen is rather certainly immature, and hence in an older specimen there may have been some degree of ossification in this area, in which, presumably, cartilage was already present. It is, however, rather certain that maturity would not have brought this area to the highly ossified condition seen in typical Embolomeri. This condition of the vertebrae has led me to erect for this form the new family Proterogyrinidae.

It is possible that the Proterogyrinidae represents a generalized type of anthracosaur, rather than a primitive group of embolomeres or embolomere ancestors. But because of the similarity in most features the Proterogyrinidae may, provisionally at least, be included in the Embolomeri.

The finding of this form, however, suggests reconsideration of generally accepted ideas of vertebral evolution in labyrinthodonts. A first major attempt at sorting out the membership of this group was that of Watson in his classic papers on the origin and evolution of the Amphibia (1919, 1926), in which he distinguished between the Rhachitomi, the Stereospondyli descended from them, and the Embolomeri. He considered the embolomeres to be the basal group of the entire Labyrinthodontia. In later years it became apparent that the story was somewhat different, and I proposed (Romer, 1947) that, leaving out of consideration the Devonian ichthyostegids, all labyrinthodonts could be divided into two major groups, Temnospondyli (including Rhachitomi and Stereospondyli) and Anthracosauria (including the Embolomeri and forms leading toward and to the Reptilia). This proposal assumed that in ancestral forms there was a large single intercentrum, centered ventrally, and

small paired pleurocentra, dorsolateral in position; that in the temnospondyls the pleurocentra remained small, and disappeared in stereospondyls, while in the Anthracosauria the pleurocentra enlarged to form the major central structure;¹ the embolomeres, as a side branch of the anthracosaurs, formed a variant in which intercentrum as well as pleurocentrum grew to form a second complete ring.

Since the publication of this thesis, nearly all more recent discoveries have tended to support it, although some variants in the temnospondyl pattern have been discovered, such as the peculiar plagiosaur group (Panchen, 1959) and *Dolesempetodon* (Bolt, 1969). The nature of the centra in ichthyostegids (Jarvik, 1952) demonstrated the high antiquity of the temnospondyl pattern. My belief that the rhachitomous type was present at an early date has been confirmed by the finding by Baird (1957) that the loxommids, which had appeared before the close of the Mississippian, were rhachitomes, and by the discovery of typical rhachitomes in the Mississippian Greer quarry, including not only the specimen I have already described (Romer, 1969) but also others awaiting description.

In 1964 I elaborated further on a probable evolutionary pattern among anthracosaurs. I assumed that, beginning with the temnospondyl type of centrum, the pleurocentra grew downward, first in the form of two half rings,² and then consolidated into a complete ring, while the intercentra remained ventral wedges. I termed this the diplomerous condition. At this stage of phylogenetic development, I believed, there occurred a dichotomy, the embolomeres splitting off and developing the intercentra as well as pleurocentra

¹ I consider here only the history of ossifications; as Panchen has pointed out (1963), either intercentrum or pleurocentrum, if it tends to take over the entire "central" area, includes in its substance the entire skeletogenous material of the segment, earlier split between the two types of element.

² A situation seen in *Pholidogaster*, which I interpreted as a primitive anthracosaur. Panchen (*in litteris*, and cf. Carroll, 1969) has disputed this, suggesting that *Pholidogaster* is a temnospondyl. The skull of the *Pholidogaster* type is too crushed to be interpretable, and Panchen believes that the anthracosaur skull in the Edinburgh collections which Watson and I thought to belong to this genus can not so be assigned. My belief in the anthracosaurian nature of this Lower Carboniferous form, however, was based mainly on the nature of the pleurocentra, which form two half-rings reaching the ventral surface of the column. Just this type of structure is seen in the immature specimens of the anthracosaur *Discosauriscus* (Spinard, 1953); temnospondyl pleurocentra are typically confined to a dorsal position, without ventral expansion.

into complete rings, while in the "main line" tending toward and to the reptilian condition (Seymouriamorpha in a broad sense), the intercentra failed to develop further and tended to be reduced.

Despite the restricted amount of material and its disassociated condition, the apparent nature of the *Proterogyrinus* column indicates that the story of anthracosaurian vertebral evolution needs reconsideration. In nearly every feature that can be made out in this new form, we are dealing with an animal closely allied to the embolomeres and perhaps to be included in that group in a broad sense. But, in conflict with my earlier beliefs, the pleurocentrum is not yet a complete ring, while the intercentrum is in an equally advanced condition. This suggests that the embolomeres split off from the anthracosaur "main line" at an earlier stage than I had thought was the case. Very probably further Mississippian discoveries at Greer and elsewhere will show that anthracosaur evolution was far more complex than I had assumed.

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OBSERVATIONS ON THE PENNSYLVANIAN CRINOID *ENDELOCRINUS ARMATURA* (STRIMPLE)

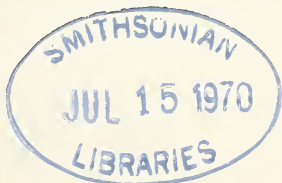
J. J. BURKE

ABSTRACT

Originally described as a species of *Delocrinus*, the Middle Pennsylvanian crinoid *Endelocrinus armatura* (Strimple) shows late attainment of biserial arm structure and has pits at the corners of the dorsal cup plates, both characteristic features of *Endelocrinus*. Unique ornamentation, predominately nodose at maturity, is traceable from pit-node structure in juveniles. Discovery of new specimens extends the geographic range of the species from Oklahoma to Ohio and Illinois.

Most species of Pennsylvanian inadunate crinoids are known only from dorsal cups; the arms are seldom preserved, either as a whole or in part. Consequently I have been fortunate in having at hand for the present study two specimens of a species of *Endelocrinus* in which most of the arms are preserved. This crinoid is characterized by unusual ornamentation, and in addition, one specimen represents a young, the other a mature stage of growth, permitting us to trace the ontogeny of the arms in at least one species of *Endelocrinus*.

For the opportunity to study these two specimens I am indebted to Dr. Richard D. Hoare of Bowling Green State University, Mr. James L. Murphy of Case Western Reserve University, and Dr. Porter Kier of the United States National Museum. I also wish to thank Dr. Kier for making the photographs from which the illustrations for this paper were taken.



SYSTEMATIC PALEONTOLOGY

Family ERISOCRINIDAE Miller, 1889

Genus **ENDELOCRINUS** Moore and Plummer, 1940**ENDELOCRINUS ARMATURA** (Strimple), 1949

Plate 1, figs. 1-6

Delocrinus armatura Strimple, 1949, *Paleontographica Americana*,
v. 3, pt. 1, p. 18, pl. 3, figs. 3, 6.

Diagnosis: A large species of *Endelocrinus* (diameter of dorsal cup at maturity exceeding 19 mm); form ratio 0.37 to about 0.41. Ornamentation distinctive, with crown plates characterized by pits and nodes; pits dominant over nodes at juvenile stage, nodes predominant and granulose ornamentation characteristic of mature stage; initiation of biseriality on third to fifth secundibrachs at cup width of about 19 mm, with "normal biseriality" attained on seventh or eighth secundibrachs. Primibrachs without spines.

Occurrence: Middle Pennsylvanian (Oklahoma, Ohio, and Illinois).

The holotype of this species was derived from the Pumpkin Creek Limestone, Dornick Hills Group, Pennsylvanian, in Love County, Oklahoma.

In the original description of the holotype, U.S.N.M. S4689, Strimple did not note the characteristic *Endelocrinus* pits at the angles of the plates of the dorsal cup and attributed this species to *Delocrinus*. At the same time he failed to indicate the unique ornament of the cup, stating only that the ornamentation "consists of irregular swollen tubercles which are more pronounced on the RR than the BB."

Of the two specimens which I am attributing to *Endelocrinus armatura*, the one which approaches nearest to the holotype in size and ornament is in the collection of the United States National Museum and was collected by Mr. James L. Murphy. It consists of a dorsal cup with the greater part of the arms and a portion of the stem attached. This specimen, U.S.N.M. 166578, was taken from the Putnam Hill Limestone of the Allegheny Group, Pennsylvanian, in the NE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 13, Springfield Twp., Muskingum County, Ohio. The Putnam Hill Limestone crops out about 200 feet west of U.S. Route 22 on a small knoll west of a shopping center designated on the Zanesville West 7.5' Quadrangle.

Because Strimple's holotype has suffered damage from weathering, breakage and dislocation of plates, it is difficult to make strictly comparable measurements of the two specimens. Measurements of height and width of U.S.N.M. S4689 are at best approximate, and I believe that the form ratio is closer to 0.41 than Strimple's finding of 0.45. The Ohio specimen is a larger and presumably older individual, with a form ratio of 0.37. Breakage and distortion may account to some extent for the apparent differences in width and depth of the basal impressions of the two specimens, but the holotype actually appears to have a wider and shallower concavity. The proportions of the radials and basals of the two dorsal cups are in close accord, and the cups are also similar in the outward flare of their radials and in showing channels along the interrarial sutures. Despite the variations noted, the remarkable agreement in peculiar ornamentation argues strongly for the specimens being conspecific.

As Strimple noted, the most prominent feature of the ornamentation of the cup is large nodes or tubercles. These are irregularly distributed for the most part, although they tend toward a festoon-like arrangement below the forefacets of the radials. The nodes are more distinct on the radials, but they are found on the basals also. However, the most striking ornamental feature of these dorsal cups consists in angular depressions associated with the nodes and connected by a network of slender and shallow canals. The depressions are most numerous on the basals, but they also occur along with the canals, on the radials. In the Ohio specimen, the proximal region of the basal circlet is more extensively ornamented. A single large, less angular depression occupies most of the surface of the portion of anal X that rises above the summit of the cup, and in U.S.N.M. 166578, the Ohio specimen, a similar depression shows on the overlying tube plate. In this specimen there also appear to be traces of incipient granular structure on portions of the cup, but none is showing within the basal impression.

Unfortunately, the holotype of *Endelocrinus armatura* consists of no more than the dorsal cup with a portion of the stem attached. The Ohio specimen, U.S.N.M. 166578, preserves, in contrast, a considerable portion of the arms. A glance at the arms leaves no doubt that this is a very young individual. The height of the axillary first

primibrachs and the markedly high and quadrangular proximal secundibrachs are evidence of this.

The primibrachs of this young specimen display the same ornamentation as the dorsal cup, with variations. The depressions are more rounded and predominate over the nodes in diameter. There are one or two crater-like impressions on each flank of a primibrach. Canals are also present. The primibrachs lack spines. Near the distal tip of the primibrach of the A ray there is a depression from the floor of which a small node originates. The nodes are prominent and little trace of the depressions remains in the primibrachs of rays C, D, and E. The primibrach of the B ray is worn at this place, but appears to have borne a small node in the depression.

For the most part, the secundibrachs remain quadrangular up to the sixth or seventh, with long and short sides alternating. Distally they become triangular or cuneate, and the initiation of the biserial arrangement is apparent on the eighth or ninth, where the cuneate plate fails to extend across the full width of the arm. None of the arms are complete; there appear to be 13 secundibrachs on one of them.

A few of the articular surfaces of the secundibrachs are showing, but some of their details are obscure. The outer ligament area is faintly denticulate and the outer ligament pit slitlike. The transverse ridge is indistinct. The intermuscular notch is V-shaped and, together with the intermuscular furrow, divides the two large flexor muscle areas.

The sides of the secundibrachs show shallow hollows, indicating that even at this early stage some interlocking of the arms was possible.

EXPLANATION OF PLATE 1

(All figures $\times 2$)

Fig. 1. *Endelocrinus armatura* (Strimple), holotype, U.S.N.M. S4689, from the Pumpkin Creek Limestone, Dornick Hills Group, Love County, Oklahoma. a, basal view and b, posterior view of the dorsal cup.

Fig. 2. *Endelocrinus armatura* (Strimple), hypotype, U.S.N.M. 166578, from the Putnam Hill Limestone, Allegheny Group, Muskingum County, Ohio. a, basal view and b, posterior view of the crown.

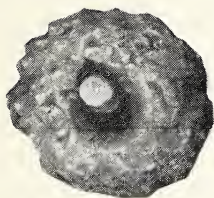
Fig. 3. *Endelocrinus armatura* (Strimple), hypotype, B.G.S.U. 2540, from the shale above the No. 6 Coal, Kewanee Group, St. Clair County, Illinois. a, basal view and b, posterior view of the crown.



1 a



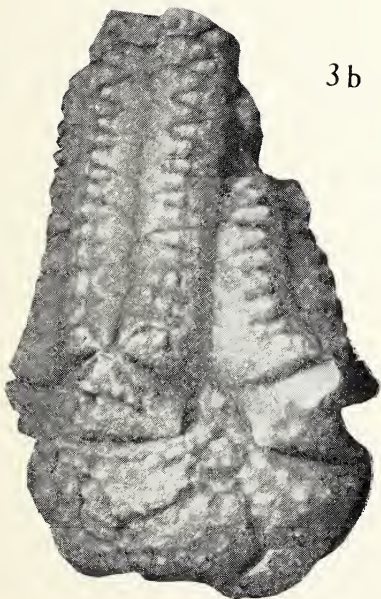
1 b



2 a



2 b



3 b



3 a

The specimen preserves a few stout pinnulars, but no complete pinnules.

Depressions and nodes also characterize the ornamentation of the secundibrachs, but only a few of these plates show canals. The first secundibrach bears more prominent nodes than those distal to it, but for the most part lacks the order in arrangement of depressions and nodes that exists in the secundibrachs that follow. This, in its simplest form, consists of a diamond-shaped depression shared by pairs of secundibrachs along the length of the arm, extending from underlying to overlying plates, with its lateral angles at their sutural junctions. The vertical angles of the depressions are usually marked by nodes or incipient nodes. There are variations of this pattern, but as the secundibrachs approach or attain the cuneate stage, the plates usually bear a single prominent node nearly marking the midline of the arm.

Here and there on the arms there appear to be traces of granular ornamentation, but it is not well defined.

The second specimen which I am referring to *Endelocrinus armatura* was collected from the shale over the No. 6 Coal of the Carbondale Formation, Kewanee Group, Pennsylvanian, at the Midwest Coal Company mine near Millstadt, St. Clair County, Illinois. It was found by Miss Dorothy Lalonde, a student of Dr. Richard D. Hoare of Bowling Green State University, who in turn submitted the crinoid to me for study.

This specimen (B.G.S.U. 2540) is part of a crown with portions of seven arms attached. Part of the stem is also preserved. On the anterior side the arm and cup plates are dislocated and mashed. An estimated width of about 19.5 mm for the dorsal cup indicates that we are dealing with a large species of *Endelocrinus*. The form ratio was probably about 0.40.

The basal impression is relatively deeper than that of the holotype of *Endelocrinus armatura*, but apparently less so than that of the juvenile specimen from Ohio. The Illinois specimen is also closer in accord with the holotype in showing less pit and node ornamentation in the proximal portion of the basal circlet; the pits and nodes are most evident in areas adjoining the distal reaches of the interbasal sutures, although they are also present on other parts of the distal extensions of the basals.

In this mature specimen the nodes predominate over the pits.

Growth of the nodes has eliminated the canals, and modified the surface to such an extent that only one of the characteristic *Endelocrinus* pits, that of the DE interray, is still evident. Nodes occupy the areas that show as pits in anal X and the overlying tube plate of the Ohio specimen, although the outlines of the pits are still apparent. The entire cup bears coarsely granulose ornament, which extends to the proximal region of the basals.

The primibrachs, in keeping with the age of this large specimen, are relatively of less height and greater width than in the juvenile specimen from Ohio. What remain of the craterlike depressions shown on the primibrachs of that juvenile individual appear only as irregular borders separating a lumpy mass of nodes from the relatively smooth lateral flanks of the plates. The most distinct of these nodes are those at tips of the primibrachs, which are relatively much larger than those characterizing the juvenile specimen and much more irregular in outline. No traces of the canals remain on the primibrachs.

The secundibrachs, for the most part, remain quadrangular up to and including the third or fourth, although in one arm only the first two secundibrachs are quadrangular. Triangular (cuneate) plates succeed the quadrangular secundibrachs, and also mark the initiation of biseriality, for these plates fail to extend the full width of the arm. However, "normal biseriality," as interpreted by Grabau (1903, p. 290) apparently was not attained before the seventh or eighth secundibrach. The arms are not complete; there are 18 secundibrachs present in each of the two with the most length preserved, and these arms must have been at least a third longer originally.

Some of the biserial secundibrachs show the articular surfaces, which are fairly typical for *Endelocrinus*. There are indications of the external ligament area, transverse ridge, intermuscular notch and intermuscular furrow. The principal flexor muscle scars are fairly evident, but the minor scars are rather obscure.

The interlocking structures of the arms are traceable not only on the sides of the arms, but also in external view, and the concave borders of one arm are seen to mesh with the convex borders of the adjacent arm with remarkable precision.

Along the midline of the arm each secundibrach bears a single prominent node—the feature noted in the juvenile specimen at the

cuneate stage. These nodes occupy what were the diamond-shaped depressions in the secundibrachs of the young crinoid. However, although the nodes on the secundibrachs, as well as on other parts of the crown of the more mature specimen have supplanted the pits and other depressions, it is still possible to find indications of the former structure in these secundibrachs.

Coarse granulose ornamentation, such as that found on the dorsal cup, also characterizes the arms of the Illinois specimen.

Linear measurements, in millimeters, of the holotype of *Endelocrinus armatura* and the two specimens which I am referring to the species are as follows:

	Holotype U.S.N.M. S4689	Hypotype U.S.N.M. 166578	Hypotype B.G.S.U. 2540
Height dorsal cup	4.6*	4.6	8.2*
Width dorsal cup	11.1*	12.3	19.5*
H/W	0.41*	0.37	0.40*
Width basal concavity	5.7*	5.0	8.4
Height basal concavity	—	1.8+	2.3+
Width stem	1.8	1.9	2.9
Length basal	3.6**	4.0	6.5
Width basal	3.9	4.2	7.7
Length radial	3.6	4.0	6.0
Width radial	5.9	6.5	8.6
Length suture between BB	2.7**	2.7	4.7
Length suture between RR	2.3	2.4	3.4
Length anal X	2.2	3.6	3.9
Width anal X	2.0	2.7	3.6
Length first tube plate	—	1.4	2.1
Width first tube plate	—	1.7	2.4
First primibrachs:			
A, length	—	4.9	5.7**
A, width	—	5.8	8.5**
B, length	—	3.8	4.8**
B, width	—	5.9	7.9
C, length	—	4.9	5.3
C, width	—	5.7	8.0
D, length	—	5.0	5.8
D, width	—	5.5	8.2
E, length	—	4.0	4.7
E, width	—	5.8	8.4

*Estimated

**Approximate

DISCUSSION

The unique major ornament of the three crinoid specimens treated here, coupled with the fact that it can be traced step by step from juvenile to mature stages of growth, constitutes the strongest argument for regarding the three specimens as conspecific. Greater size and presence of definite granular ornamentation characterize the mature individual, B.G.S.U. 2540, and there appear to be variations in depth and width of the basal impression among the three specimens involved, but I have given these characters full consideration and fail to find them grounds for specific or subspecific distinction.

In a previous paper (Burke, 1967) I suggested that fully biserial arm structure may have been attained late in life in various species of *Endelocrinus*. Study of these specimens of *Endelocrinus armatura* and additional undescribed material representative of *Endelocrinus* further supports this suggestion. However, biseriality in the arms of B.G.S.U. 2540 has progressed at least to the extent that I have observed the condition in certain presumed mature specimens of *Delocrinus*. Nevertheless, biserial arm structure must have been realized at a very early stage of growth in most species of *Delocrinus*—possibly even before the arm segments were sufficiently developed to remain associated after the death of the individual, otherwise crowns showing earlier stages in attainment of biseriality would be known.

There is, however, one species, either a *Delocrinus* or a form closely related to that genus, which may compare with *Endelocrinus* in delayed acquirement of biseriality. Strimple and Knapp (1966, pl. 36, figs. 1, 2) have illustrated the crown of a specimen which they attribute to "*Diphuicrinus*" *croneisi* Moore and Plummer, from which they conclude, because the arms are uniserial, that "*Diphuicrinus*" is distinct from *Delocrinus*. However, the distal secundibrachs of the crown appear to be cuneate, which strongly suggests that the individual might have eventually developed biserial arm structure. Furthermore, if Strimple and Knapp are correct in their identifications, this is presumably a young individual; the diameter of the dorsal cup is given as 21 mm, that of the holotype of the species as 24 mm; cup diameters of two other specimens, however, are noted as 31 and 43 mm respectively (ibid., p. 313). If the latter two specimens actually pertain to the species, there would

appear to be the possibility that in attaining such size "*Diphocrinus*" *croneisi* might also have acquired some degree of biserial arm structure.

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NUMBER 12

MAUCHCHUNKIA BASSA, GEN. ET SP. NOV.,
AN ANTHRACOSAUR (AMPHIBIA, LABYRINTHODONTIA)
FROM THE UPPER MISSISSIPPIAN

NICHOLAS HOTTON III
Smithsonian Institution

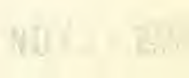
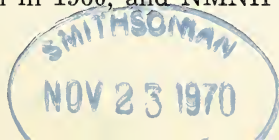
ABSTRACT

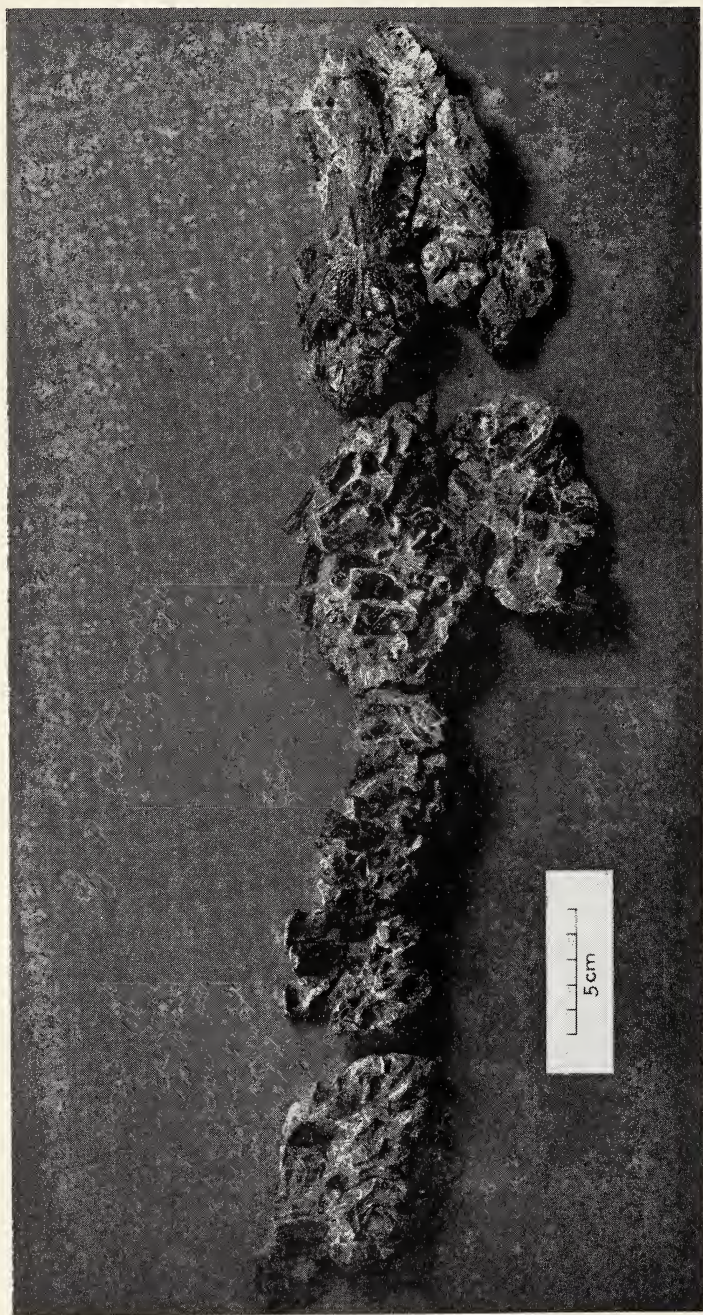
The skull, articulated presacral vertebral column, and several limb elements of an anthracosaurian amphibian from the lowest beds of the Mauch Chunk Group (Upper Mississippian) at Greer, West Virginia, are described as *Mauchchunkia bassa*, gen. et sp. nov., and made the type of a new family, the Mauchchunkiidae. In most respects the type resembles the Embolomeri, but the presacral column is short, the intercentrum is a ventrally placed crescent, the limbs are stout, and the snout is not elongate. *Mauchchunkia* appears to be the most generalized anthracosaur yet described, and in many of its features it supports the view that the primary adaptation of primitive tetrapods was toward a terrestrial environment. Vertebral structure foreshadows reptilian conditions, and the Mauchchunkiidae are proposed as early ancestors of all reptiliomorph tetrapods.

INTRODUCTION

The specimen at hand, catalogue number 22573 in the National Museum of Natural History (pl. 1), is the third reasonably complete fossil tetrapod to be described from the Upper Mississippian deposits at Greer, Monongalia County, West Virginia. At the present time the fossils from Greer are, except for *Ichthyostega* of the latest Devonian (Säve-Söderbergh, 1932), the oldest tetrapods of which we have detailed information, and provide almost the only record between *Ichthyostega* and the much better known tetrapods of the Pennsylvanian (Panchen and Walker, 1961; Romer, 1969).

The first tetrapod remains from Greer were evidently discovered by an amateur, Mr. L. R. Collins, in 1948, whose find was followed up successfully by Mr. John J. Burke and Mr. William E. Moran. My attention was first drawn to the Greer locality by Mr. Moran in 1960, and NMNH 22573 was collected during a trip that





Mauchchunkia bassa Hotton. Photograph showing skull and articulated vertebrae of the holotype, NMNH 22573, from the Bickett Shale, Mauch Chunk Group, Mississippian, at Greer, West Virginia.

Mr. Moran and I made to Greer in November of that year. It is with pleasure that I acknowledge my debt to Messrs. Moran and Burke for their generous cooperation, not only in showing me the locality but also in educating me to the potential of late Paleozoic deposits of West Virginia. Thanks are also due to officials of the Greer Limestone Company for their friendly cooperation in permitting access to the quarry, and to Dr. Alec Panchen of the University, Newcastle-upon-Tyne, to Dr. Robert Carroll of McGill University, and to Professor A. S. Romer for their open-handedness in providing access to unpublished material.

PROVENANCE

The Greer locality is in a quarry operated by the Greer Limestone Company in the valley of Deckers Creek, Monongalia County, West Virginia, about 6.5 miles southeast of Morgantown. The quarry lies just north of State Route 7, on the west side of the confluence between a small tributary valley and Deckers Creek valley. The actual spot in which the bones were found is about 0.5 miles north of the highway along the west side of the tributary valley. NMNH 22573 was found in place in dark greenish-gray shales overlying the massive limestone that is being worked commercially at Greer.

Romer (1969) states that the rock being quarried commercially is recognized by the West Virginia Geological Survey as the Union Limestone of the Greenbrier Group (see also Weller, et al., 1948). The uppermost beds of the Greenbrier, the Cypress Sandstone and Alderson Limestone, are missing at Greer (Tilton, 1928), so that the Union is directly overlain by the greenish and reddish shales and blue to gray limestones that belong to the Bluefield Formation, the lower subdivision of the Mauch Chunk Group.

The lowest 30 feet of the Bluefield are readily identified, on the basis of Tilton's detailed description, at the spot from which NMNH 22573 was collected (pl. 2). In the center of the picture, the boy is standing in the excavation left by removal of the specimen, about 6 feet above the bottom of the Bickett Shale. The Bickett (Bi) is about 13 feet thick at Greer; its bottom is just below the top of the vegetation in the foreground, and its top is about 1 foot below the lower ends of the crossed tree trunks at the upper left of the picture. It is underlain by the Glenray Limestone (Gl), the massive layer near the lower right of plate 2. The Glenray is 7 to 10 feet thick in various parts of the quarry; its base is buried at this spot. Below the Glenray lies 6 feet of Lillydale Shale, covered by rubble in the foreground but recognizable close by. The Lillydale lies directly upon the Union at Greer.



Bluefield Formation, Mauch Chunk Group, exposed at Greer, West Virginia.
Gl, Glenray Limestone; Bi, Bickett Shale; Re, Reynolds Limestone.

Above the Bickett, marked by the dark band below the crossed tree trunks in plate 2, is a limy layer containing abundant brachiopods, some of which were identified by G. Arthur Cooper as *Anthracospirifer*, *Orthotetes*, and *Diaphragmus*. This is evidently the bottom of the Reynolds Limestone (Re), identified as "Orthotetes Zone" by Tilton (1928).

Most of the vertebrate remains collected thus far evidently come from three or four feet below the level of NMNH 22573. Fish remains are generally fragmentary; partly articulated material is restricted to lungfish (D. H. Dunkle, written communication, 1969) and tetrapods. A few carbonized plant fragments are found at these levels, and clay pebbles are common in the matrix immediately surrounding articulated vertebrate elements. No ripple marks have yet been noted in the Bickett at Greer. Invertebrate remains are rare and fragmentary at the vertebrate-bearing levels, and no marine forms have yet been identified with certainty. The Bickett becomes more limy toward the top and marine vertebrates appear in it; change from vertebrate levels to the overlying limestone is thus gradational.

Clay pebbles and fragmentary fish remains indicate that the environment in which the Greer tetrapods occur was one of flowing water, and it is probable that all of the material suffered some transportation before burial. However, the association of elements of single individuals, and the articulation of NMNH 22573, suggest that these specimens were not transported far. All of the articulated or associated remains represent terrestrial, aquatic forms, which indicates that the portion of the Bickett Shale that contains them is an atypical facies of the normally marine Mauch Chunk Group. At Greer the middle part of the Bickett evidently represents a local and momentary phase of terrestrial deposition, probably a consequence of the formation of a temporary bar in shallow marine waters and not of any change in tectonic activity. It was terminated gradually as continuing tectonic subsidence brought about the return of more nearly normal marine conditions at the site.

SYSTEMATIC PALEONTOLOGY

Class AMPHIBIA

Order ANTHRACOSAURIA

Family MAUCHCHUNKIIDAE fam. nov.

Diagnosis: Anthracosaurian labyrinthodonts that resemble embolomeres in pattern and sculpture of dermal skull bones, and general structure of skull, neural arches, and limbs. Differ from embolomeres and Proterogyrinidae (Romer, 1970) in that intercentrum is crescentic in shape and unossified dorsally, attaining to not more than half the height of the fully ossified pleurocentral disc. Differ from embolomeres in that presacral column is short (not more than 28 segments), limbs stout, snout not elongate. Supratemporal bone contributes significantly to anterodorsal margin of otic notch. Type genus *Mauchchunkia*.

Genus *Mauchchunkia*¹ gen. nov.*Mauchchunkia bassa*² sp. nov.

Pl. 1; Figs. 1-14

Diagnosis for genus and species: An anthracosaur of moderate size in which pre- and postorbital moieties of the narrow skull are subequal in length. Postparietal bone more than half the length of parietal. Anterior maxillary teeth appreciably higher crowned than posterior; diminution of crown height from front to rear gradual. Approximately 26 marginal teeth. Palatal dentition closely similar to that of the embolomere *Eogyrinus attheyi* as restored by Panchen (written communication, 1969), with two tusk-and-pit pairs on palatine and a single smaller pair on ectopterygoid, followed by four smaller teeth comparable in size to marginals. Pineal opening suboval, rimmed; slight ridge formed along interparietal suture as in the embolomere *Pteroplax cornuta*.

Holotype: National Museum of Natural History 22573. Nearly complete skull in which dermal elements are partially disarticulated and broken. Braincase badly damaged, partially hidden. Lower jaw nearly complete but broken. Twenty-seven vertebrae, including atlas-axis complex, articulated but with neural arches displaced and broken. Dermal shoulder girdle in approximately correct relationship to column but smashed; large fragments of bone associated with it pertain to scapulocoracoid but are too poorly pre-

¹ The generic name is derived from the stratigraphic occurrence.

² Specific designation refers to the fact that the holotype occurs near the bottom of the Mauch Chunk Group.

served to permit more than tentative analysis. Heads of right and left humeri, and abundant fragments of ribs and dermal armor also present.

Referred specimens: National Museum of Natural History 26368. Left and right humeri, minus heads, left and right radii, left ulna, four metapodials and four phalanges more closely associated with left limb elements than with right, one metapodial associated with right limb.

National Museum of Natural History 26369. Fragments of three neural arches and right ilium and pubis, and proximal ends of left and right femora.

Horizon and locality: Six feet above the bottom of the Bickett Shale, Bluefield Formation, Mauch Chunk Group, Upper Mississippian, at Greer, Monongalia County, West Virginia, in the face of a quarry operated by the Greer Limestone Company, about 0.5 miles north of West Virginia Highway 7.

PRESERVATION AND RESTORATION

The holotype of *Mauchchunkia* was collected as a group of limy nodules with bits of bone exposed on the surfaces. The skull had come to rest right side up, but during burial it had collapsed to the left, folding up along the typical anthracosaur hinge-line between temporal series and squamosal, so that the left cheek and lower jaw are folded underneath, covering part of the palate; the right cheek and lower jaw are spread out to the right.

Dermal elements of the skull roof are in some disarray because of maceration. Both squamosals and the premaxillary region have been severely crushed so that details of their morphology cannot be made out, and details of the area immediately in front of the orbits are also obscure. Restoration of the remainder of the skull is based upon actual sutures or upon patterns of dermal sculpture, and may be accepted with confidence.

Most of the palate is represented merely by broad expanses of bone covered with a shagreen of very fine denticles, and sutures cannot be determined. Fortunately, a part of the pterygoid adjacent to the basiptyergoid articulation is preserved in proper relationship to the most posterior ectopterygoid teeth, so that the width of the pterygoid in this region can be determined, at least to an order of magnitude. This width has provided the basis for establishing the width and depth of the skull as restored.

In the axial skeleton, both central and neural arch elements have been shifted variously, chiefly in a lateral direction; some

intercentra are missing, and all of the neural arch elements are more or less broken. To the extent that the broken and displaced elements have been restored to their proper relationships, the illustrations represent reconstructions. All of the vertebrae are preserved in their proper sequence, however, and proportions of individual bones are readily determinable.

The entire pectoral girdle is preserved in NMNH 22573 but was badly smashed before and during fossilization. In addition, the ventral surfaces of clavicles and interclavicle are partially obscured by masses of abdominal scales, and the dorsal surfaces by a string of about seven vertebrae and ribs. Restorations shown in figures 9 and 10 are reliable with respect to most dimensions, but the outlines of the interclavicle and the shape of its stem, and the shape of the top of scapula and cleithrum are uncertain.

Except for the heads of the humeri and one anterior phalanx, no limb elements are preserved with the holotype of *Mauchchunkia*. Restoration of the front limb is based upon NMNH 26368. This specimen was found in a small tumble-block near the holotype, but it was not in place and its association is open to question. It is referred to *Mauchchunkia* because the headless humeri are precisely the right size for the humeral heads that belong to the type, and their ends are broken at the proper angle to fit the broken ends of the heads, although they do not make an exact "jigsaw puzzle" fit. Moreover, the bones of NMNH 26368 were covered with a limy crust before preparation, as were the bones of the type. Most other specimens from Greer that I have examined lack a nodular crust, and instead lie free in the shale matrix.

NMNH 26369 originally consisted of a small limy nodule with broken bones exposed in its surface. It was forwarded to the writer by Mr. Burke with the note that Mr. Moran had found it in the excavation from which the holotype of *Mauchchunkia* had come. Its association is thus better than that of NMNH 26368, and the pelvic and femoral fragments that it contains represent an animal of the same size as the holotype.

MORPHOLOGY

Skull roof: In dorsal aspect (fig. 1) the skull presents the appearance of a typical anthracosaur, with characteristic sculpture, prominent otic notches, and small but distinct tabular horns. The intertemporal bone is almost as large as the supratemporal, and the tabular has a broad contact with the parietal. In dermal pattern and sculpture the skull resembles that of "*Paleogyrinus*" *decorus*, but the tabular horns, projecting as they do from the undersides of the tabulars, are more nearly similar to the tabular horns of *Ptero-*

plax cornuta. The orbits lie about halfway along the length of the skull, which is narrower relative to its length than the skull of either "*Paleogyrinus*" or *Pteroplax*; gross proportions are more nearly comparable to those of a form like *Gephyrostegus* than to most embolomeres.

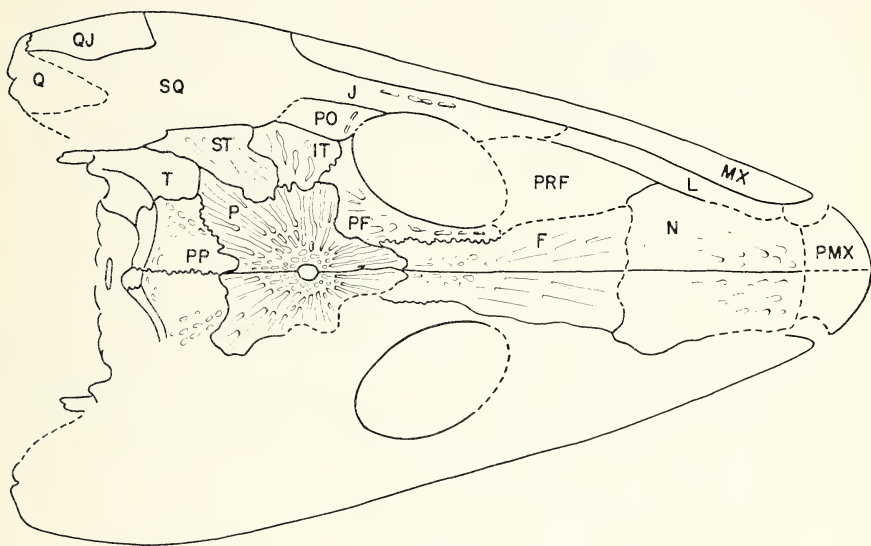


Fig. 1. *Mauchchunkia bassa* Hotton, NMNH 22573. Skull, dorsal aspect, somewhat restored. Key to elements: F, frontal; IT, intertemporal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; P, parietal; PF, postfrontal; PMX, premaxilla; PO, postorbital; PP, postparietal; PRF, prefrontal; Q, quadrate; QJ, quadratojugal; SQ, squamosal; ST, supratemporal; T, tabular, $\times \frac{3}{4}$.

The otic notch is elongate in that its dorsal margin includes part of the supratemporal as well as the tabular, instead of the tabular alone as in embolomeres. In this respect it resembles *Gephyrostegus* and other reptiliomorph anthracosaurs. As preserved, the otic notch is smashed down over the squamosal, so that its inferior margins are indeterminate. The otic margin of the squamosal (fig. 2) is restored after that of "*Paleogyrinus*" *decorus* (Panchen, 1964). It is possible, though not probable, that this margin in life was more concave than is shown in the restoration, in which case the otic notch would be larger and would bear a closer resemblance to that of *Gephyrostegus*.

A slender process of the squamosal extends ventroposteriorly between the quadratojugal and the quadrate, as in *Gephyrostegus*. The quadrate is high, and is broadly exposed posteriorly between the squamosal and the quadrate ramus of the pterygoid (fig. 1).

Its posterior surface is smooth and unsculptured, as though it contributed to the floor of the middle ear.

The anterior margins of the nasals and the entire premaxilla were badly smashed before fossilization; the anterior margin of the premaxilla is marked only by a few displaced teeth. Configuration of the external nares is unknown. They are restored as though they were superficially continuous with the skull margin, following Panchen's treatment of "*Paleogyrinus*" (1964), because the anterior margin of the maxilla appears to be intact and to consist of finished bone.

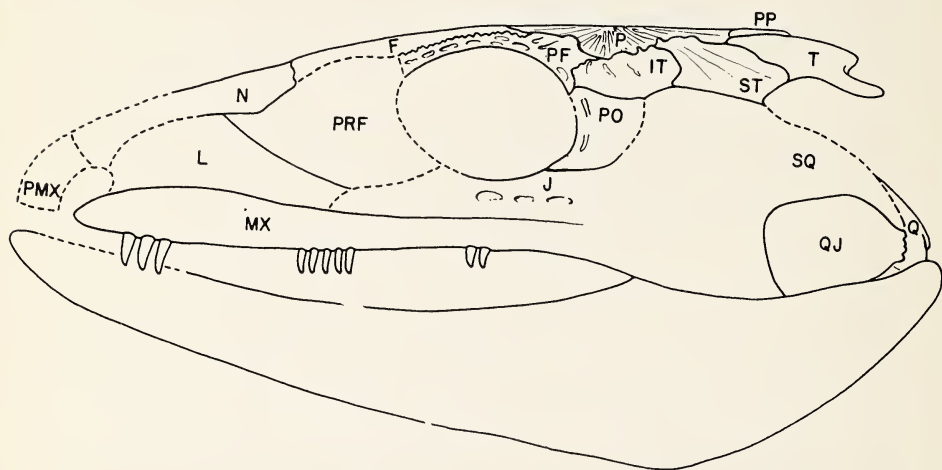


Fig. 2. *Mauchchunkia bassa* Hotton, NMNH 22573. Skull, lateral aspect, somewhat restored. For key to elements see Fig. 1. $\times \frac{3}{4}$.

The frontals are long and narrow, widening anteriorly as in "*Paleogyrinus*", and the parietals are deeply notched laterally by the large supratemporals.

Mauchchunkia is more primitive than any other anthracosaur in the relative lengths of the dermal bones of the midline series. Combined length of postparietals and parietals (skull table) is about 73 percent of the combined length of frontals and nasals (face), and the postparietal is about $\frac{2}{3}$ the length of the elongate parietal, much longer than in any Paleozoic tetrapod except *Ichthyostega* and its allies. For comparison, values of the ratio of skull table to face in embolomeres and their close relative *Proterogyrinus* (Romer, 1970) are: "*Paleogyrinus*", a relatively short-faced form, 56 percent; *Proterogyrinus*, a contemporary of *Mauchchunkia*, 50 percent; *Pteroplax*, *Eogyrinus*, and other large forms, 38 percent; *Archeria*, 33 percent or less. In these forms the relative shortening of the skull table is primarily a consequence of elonga-

tion of the snout, while in *Gephyrostegus*, in which the ratio is about 38 percent, shortening does not involve modification of gross proportions of the skull, but is related to a more deep-seated restructuring of the braincase (cf. Westoll, 1943).

The parietals are the most heavily sculptured bones of the skull, but even here the sculpture is shallow and ill defined. The frontals and nasals are almost smooth, and sculpture on the postparietals and tabulars consists of little more than a slight rugosity. Lateral line canals are almost entirely lacking. The only structures that could be so interpreted are a few linearly arranged, elongate pits surrounding the orbit (fig. 1), on the front of the prefrontal, on the postorbital, and on the jugal.

Occiput and braincase: The only relationships that have been preserved in the occiput (fig. 3A) are those of postparietals and tabulars. Restoration of the positions of exoccipital, opisthotic, and prootic (fig. 3B) must be regarded as tentative because of the damage and dislocation that these elements have suffered. The bones identified as exoccipital and opisthotic are stout, massive structures that lie, disarticulated, in the matrix behind the posterior margin of the skull, on either side of the midline.

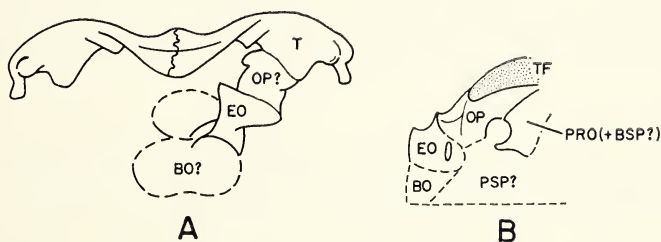


Fig. 3. *Mauchchunkia bassa* Hotton, NMNH 22573. A, occiput; B, right lateral aspect of braincase; both extensively restored. Key to elements: BO, basioccipital; BSP, basisphenoid; EO, exoccipital; OP, opisthotic; PRO, prootic; PSP, parasphenoid; T, tabular; TF, facet on opisthotic for articulation with tabular, $\times \frac{3}{4}$.

The putative exoccipital lies just behind and a little below the putative opisthotic. Ventrally it bears a posteriorly directed pedicel that terminates in an elliptical articular facet that looks like (and lies in the proper position for) the exoccipital moiety of the occipital condyle. Anterior to the base of the pedicel it is pierced transversely by a narrow canal, which, if the articular facet has been properly identified, must be the hypoglossal foramen (fig. 3B). The medial margin of this bone is finished and provides a curved surface that is plausibly interpreted as the lateral wall of the foramen

magnum. The dorsal surface is expanded into an ovate facet of a size to fit the broad posterior base of the bone identified as opisthotic (fig. 3A).

The opisthotic is so identified because the surface that is uppermost, as the bone lies in the matrix, is a falciform articular area like the dorsolateral facet on the opisthotic of "*Paleogyrinus*" (Panchen, 1964). This facet is only slightly displaced from the ventromedial margin of the occipital flange of the right tabular, and is of the proper size to articulate with that margin.

Below the right tabular is a piece of broken bone which bears a deep, well-finished notch in the margin that lies upward. If this fragment is rotated counterclockwise about 90°, so that the notch comes to face posteriorly, it fits well as a prootic (fig. 3B). The notch can then be interpreted as the anterior margin of the fenestra ovalis, which now lies in the correct position with respect to tabular and otic notch.

As restored, the occiput corresponds generally to that of "*Paleogyrinus*", except that the supraoccipital is unossified. The lateral column formed by exoccipital and opisthotic is much taller, making the braincase seem too tall and narrow in posterior aspect. However, the dimensions of the occipital condyle produced by this restoration fit the central part of the atlas-axis complex perfectly, and there would scarcely be room above the condyle for a foramen magnum of appropriate size if the braincase were not as tall as here restored.

Palate: Exposed surfaces of the palate (fig. 4) are uniformly covered by a shagreen of fine denticles and no sutures are visible. Restoration is based upon general embolomere structure. The palatine-ectopterygoid suture is placed in front of the posterior tusk-and-pit pair because of the distance between it and the next anterior pair. In distribution and form of palatal teeth *Mauchchunkia* resembles Panchen's restoration of *Eogyrinus attheyi* (written communication, 1969). In front of the anterior tusk-and-pit pair there is a tiny notch of what appears to be finished bone, which is interpreted as the medioposterior margin of the internal naris.

The area in which the pterygoid articulates with the basis cranii is identifiable by a finished medial margin and a small flange turning upward and medially from the top of the pterygoid. This flange is either the anterior root of the dorsally directed otic wing of the pterygoid, or the base of the epipterygoid below the basipterygoid articulation. But except for the flange, the entire area is crushed flat, and the remainder of the epipterygoid and otic wing

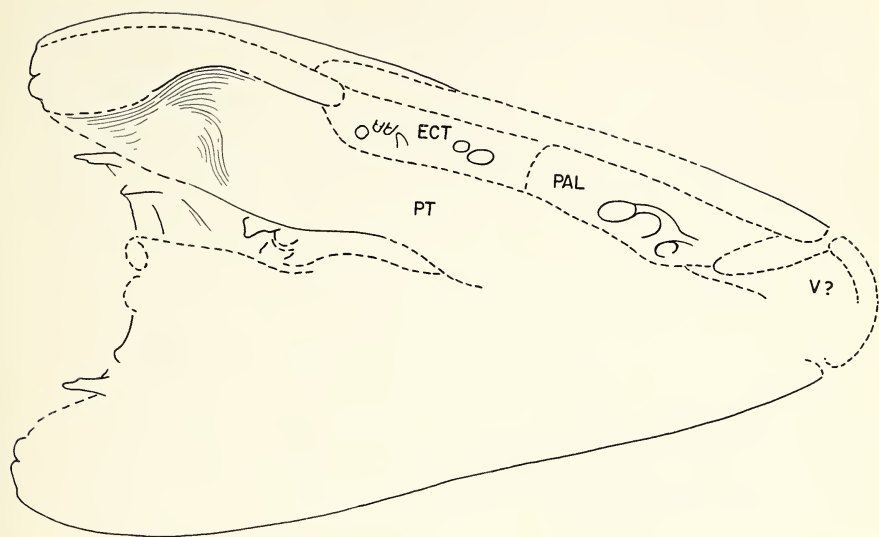


Fig. 4. *Mauchchunkia bassa* Hotton, NMNH 22573. Palate, completely restored on basis of distribution of palatal dentition, and medial pterygoid margin depicted by solid line. Key to elements: ECT, ectopterygoid; PAL, palatine; PT, pterygoid; V, vomer, $\times \frac{3}{4}$.

of the pterygoid are represented only by comminuted bits of flat bone.

A small part of the margin of the subtemporal fossa can be made out, and it is probable that the medial margin of the fossa was turned down as a vertical flange as in labyrinthodonts generally. However, poor preservation renders the exact shape of the subtemporal fossa extremely uncertain.

Teeth and lower jaw: There are about 26 marginal teeth including those of the premaxilla, and the anterior maxillary teeth are the largest. Crown height diminishes gradually from the anterior to the most posterior maxillary teeth, the position of which is shown beneath the orbit in figure 2. The dentary tooth row is essentially a mirror image of the maxillary tooth row. The lower jaw is typically anthracosaurian, lacking a retroarticular process and tapering forward from its deepest point below the coronoid region. Sutures are undeterminable. The deepest part of the jaw is slightly pitted toward its lower margin, whence shallow grooves radiate in all directions. The lateral face of the dentary is marked by shallow longitudinal grooves and elongate pits, and the symphyseal region by very small, deep pits.

Axial skeleton: The blocks in which the vertebral column was preserved can be joined as a continuous string with but one gap (pl. 1), which resulted from damage during collection. It is doubtful that any segments are missing in the region of poor contact, and the total number of relatively complete, articulated vertebrae, including atlas-axis complex, is 27. The intercentrum and part of the pleurocentrum of the 28th vertebral segment are also articulated to the back of the last block.

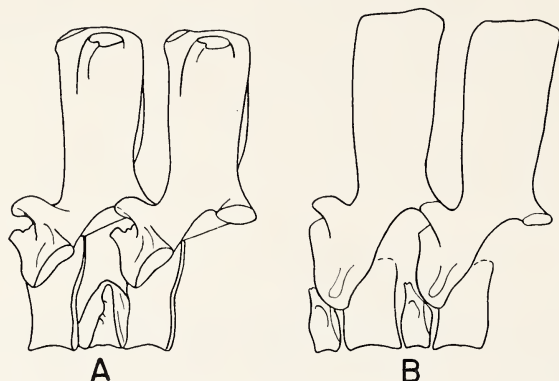


Fig. 5. *Mauchchunkia bassa* Hotton, NMNH 22573. Dorsal vertebrae, left lateral aspect, slightly restored. A, 19th segment, pleurocentrum and neural arch duplicated; B, 24th and 25th segments, $\times \frac{3}{4}$.

Except for the first four cervical vertebrae, changes in morphology of the central elements are gradual from front to back over the distance preserved. Anteriorly the pleurocentrum and intercentrum are subequal in length (fig. 5A), and posteriorly the length of the pleurocentrum is increased at the expense of the intercentrum (fig. 5B). The dorsal pleurocentra are biconcave notochordal discs in which the articulating surface is ovoid, the dorsoventral axis being slightly longer than the transverse (fig. 6B). The discoidal portion of the pleurocentrum is surmounted by a low, stout bony superstructure, the anterior face of which is convex and receives the pedicels of the neural arch (fig. 6A, B). The intercentrum forms a crescent lying below the notochord (fig. 6C). Throughout most of the column, the horns of the crescent do not reach more than halfway up the face of the pleurocentrum, and there does not appear to have been any osseous contact between intercentrum and the pedicels of the neural arch.

The convex posterior surface of the intercentrum evidently articulated with the slightly concave anterior face of the pleurocentrum of the same segment like a ball-and-socket joint, as suggested by Panchen (1966) for the embolomere *Eogyrinus*. In any

case, the anterior and posterior faces of the intercentra of *Mauchchunkia* are identically shaped and finished, and whatever the articulation was between the intercentrum and the pleurocentrum of the next anterior segment, the articulation between the intercentrum and its own pleurocentrum must have been similar. It appears that in *Mauchchunkia* as in *Eogyrinus* about the same degree of movement was possible between intercentrum and pleurocentrum of the same segment as between intercentrum and the pleurocentrum of the next anterior segment.

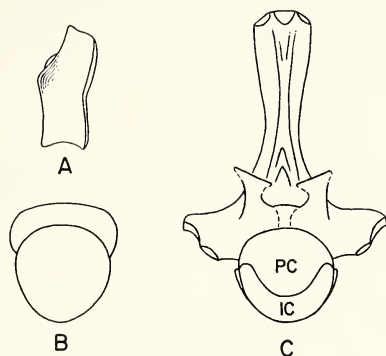


Fig. 6. *Mauchchunkia bassa* Hotton, NMNH 22573. Nineteenth vertebra. A and B, pleurocentrum, left lateral and anterior aspects respectively; C, entire vertebra, anterior aspect. Key to elements: PC, pleurocentrum; IC, intercentrum, $\times \frac{3}{4}$.

Neural arches are generally like those of embolomeres. The zygapophyses are pedicellate and lie close to the midline, and their articular facets are markedly slanted (fig. 6C). The spines are thin (of small transverse dimension) and broad (of large anteroposterior dimension), so that in cross-section they are fusiform. They are taller than the length of the arch from pre- to postzygapophysis (table 1). In this respect *Mauchchunkia* resembles such low-spined pelycosaur as *Ophiacodon* and *Stereophallodon* (Romer and Price, 1940), and contrasts with *Eogyrinus* (Panchen, 1966) and *Archeria* (NMNH 22811), in which the spines are shorter than pre- to postzygapophyseal length.

Stout, blunt processes are developed in extremely variable fashion near the tops of the lateral faces of most spines (fig. 5A). Their position is so variable that on a single spine the left process may be close to the anterior margin while the right is close to the posterior. Figure 5A illustrates approximately the highest degree of development, which grades downward to complete absence (fig. 5B). Distribution is evidently random; processes are certainly pres-

ent on numbers 3-5, 7-9, and 19 (counting back from the atlas), and are certainly absent from numbers 6, 18, 20, 22, 25, and 27. In its highest development the process is characterized by a dorsally directed, unfinished ovoid surface that is separated from the unfinished dorsal end of the spine by a narrow channel of unfinished bone. Ventrally the process fails into the lateral face of the spine, but may be continued ventrally for a variable distance as a low ridge directed toward the posterior margin of the transverse process. This ridge may mark the attachment of the myoseptum, which presumably passed down the lateral face of the neural spine, crossed the neural arch by running forward along the rib articulation (to include the rib in the plane of the septum), and terminated, via the head of the rib, on the intercentrum, as Panchen (1967) has reconstructed it in various early tetrapods.

The ribs of *Mauchchunkia* are fairly slender and appear to be approximately cylindrical throughout their length, as in embolomeres. In any case, there is no evidence of distal flattening, development of uncinat processes, or overlap in the fashion of *Ichthyostega* or the terrestrial temnospondyles.

The number of presacral vertebrae cannot be determined by the actual position of the sacrum or pelvis, for these elements are missing in the type of *Mauchchunkia*, and there are no central elements or neural arch pedicels associated with the pelvic material of NMNH 26369. However, the change in the structure of neural arch pedicels and rib articulations from front to back is closely comparable to Panchen's restoration of *Eogyrinus* (1966), in which the position of pelvic fragments and sacral rib is known. In *Mauchchunkia*, the pedicels of anterior neural arches are markedly widened, and become in effect thick, stocky transverse processes (fig. 5A, 6C). Accordingly, the anterior ribs are characterized by an elongate head that lies a considerable distance medial to the tuber-

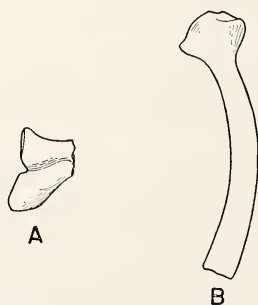


Fig. 7. *Mauchchunkia bassa* Hotton, NMNH 22573. A, head of intermediate rib; B, posterior(?) presacral rib, $\times \frac{3}{4}$.

culum (fig. 7A) in order to articulate with the intercentrum. From the 24th vertebra on back, the pedicels are expanded only slightly beyond the margins of the centrum, and in the posterior ribs the head does not project beyond the tuberculum (fig. 7B). This type of unexpanded neural arch pedicel and short-headed rib is said to be restricted to a few segments in front of the sacrum in *Eogyrinus*. The pedicels of the 24th and 25th vertebrae of *Mauchchunkia* (fig. 5B) are even less widely expanded than those of the immediately presacral vertebrae of *Eogyrinus* (Panchen, 1966, fig. 5c, d), and therefore must be very close to the posterior end of the presacral column. The pedicels of the 26th vertebra and possibly also those of the 25th are very closely-knit, perhaps co-ossified, with their respective pleurocentra.

The costal articulation of the 26th vertebra is not specialized for a sacral rib, nor does the 26th pleurocentrum show any modification for a sacral rib comparable to the sacral vertebra of *Eogyrinus*. The pedicel and pleurocentrum of the 27th vertebra are not well enough preserved to determine presence or absence of such specializations, but both the 26th and 27th pleurocentra are very massive, while the 28th is shorter and slighter than the others. It therefore seems probable that the sacral vertebra is number 27, although it could even be number 26, in the unlikely event that the sacral rib was not as highly specialized in *Mauchchunkia* as in *Eogyrinus*. A presacral vertebral count of 26 is evidently close to the mark for *Mauchchunkia*, and even if we allow for one or two missing vertebrae in the column as preserved the count cannot exceed 28.

The atlas-axis complex is complete except for the atlantal neural arch and the proatlas (fig. 8A). Central elements are little differentiated from those of more posterior vertebrae, and such specializations as they show suggest the condition of pelycosaur. The atlantal pleurocentrum is much shorter than the others, the long axis of its articular face is transverse rather than vertical (fig. 8B),

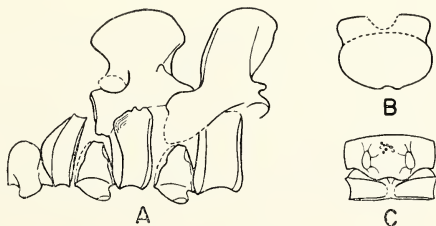


Fig. 8. *Mauchchunkia bassa* Hotton, NMNH 22573. A, atlas and axis and third cervical vertebra, left lateral aspect, positions somewhat restored; B, atlas pleurocentrum, anterior aspect; C, atlas intercentrum and pleurocentrum, ventral aspect, $\times \frac{3}{4}$.

and its anterior surface is convex. However, it is a complete disc, unfused with the axial intercentrum. The atlantal intercentrum differs from all others in that its posterior face is markedly concave, receiving the convex surface of its pleurocentrum (fig. 8A). Its ventroposterior margin forms a flange that wraps around the underside of the front of its pleurocentrum (fig. 8A, C). The lateral tips of the atlantal intercentrum are lower than those of other intercentra.

The axial neural spine is broad, stout, and hatchet-shaped, very like the axial neural spine of *Ophiacodon*. The axial prezygapophysis is "reversed", its articular facet facing upward and outward, which suggests that *Mauchchunkia* had an atlantal neural arch and presumably a proatlas of primitive reptilian configuration.

The pleurocentra of the axis and third cervical are unspecialized, and the intercentra of these two segments differ from those more posterior only in the presence of prominent ventrolateral bosses, which presumably provided articulation for cervical ribs. No other costal articular surfaces are preserved on the cervical vertebrae.

The neural spines of the third (fig. 8A) and fourth vertebrae are somewhat shorter and narrower than more posterior spines, and have a pronounced backward slant. The next two neural spines (fifth and sixth vertebrae) are distinctly narrower than more posterior spines and may retain something of the backward slant of the third and fourth. This suggests that at least six vertebrae were differentiated as cervicals to some degree. The third cervical bears a small, posteriorly directed process on the pedicel of the postzygapophysis. Nothing of the sort is preserved on any other vertebra.

Pectoral girdle: The clavicles are marked by a distinctive system of arcuate grooves which terminate toward the lateral margins of the bones in a series of shallow pits (fig. 9). They lie rather far apart, and the surface of the broad, flat interclavicle exposed between them is uniformly sculptured with shallow pits, indicating that the wide separation of the clavicles is the condition that obtained in life. Posteriorly the interclavicle is nearly smooth.

Dimensions of the cleithrum as restored (fig. 10) are reliable, but details of its structure are obscure. The restoration of the scapulocoracoid (fig. 10) is a composite, consisting of the blade of the left scapula above the supraglenoid foramen and the battered anterior margin of the right coracoid. The glenoid region is preserved only as abraded pieces of massive bone surrounding the head

of the right humerus, from which the dimensions of the glenoid have been restored. The composite scapulocoracoid resembles that of *Archeria* except that the blade of the scapula is somewhat lower and narrower.

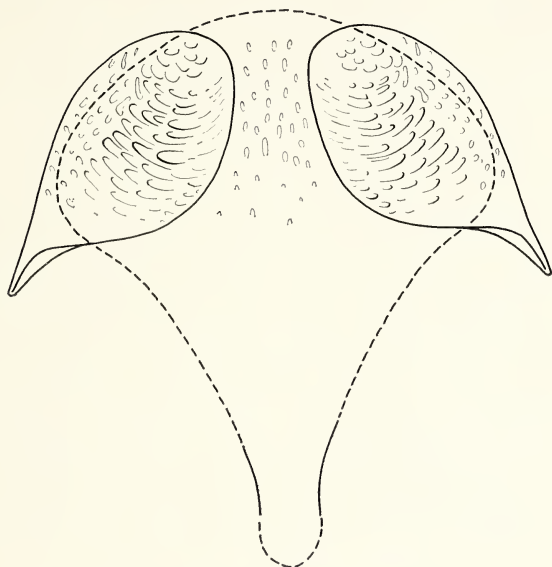


Fig. 9. *Mauchchunkia bassa* Hotton, NMNH 22573. Dermal shoulder girdle, ventral aspect, extensively restored, $\times \frac{3}{4}$.

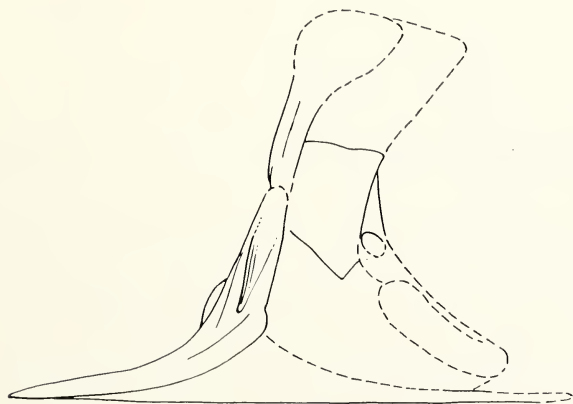


Fig. 10. *Mauchchunkia bassa* Hotton, NMNH 22573. Cleithrum and scapula, left lateral aspect, extensively restored, $\times \frac{3}{4}$.

Pelvic girdle: The only identifiable parts of the pelvis are the acetabular contribution and stem of the ilium, and a small fragment of the pubis which includes the obturator foramen. These fragments are fitted into a restoration of the pelvis (fig. 11) based upon that of *Archeria* (Romer, 1957). A notable feature of the iliac portion of the acetabulum is that its articular face is directed primarily downward and is very heavily buttressed dorsally, as though to support the weight of an animal that spent much of its time out of water.

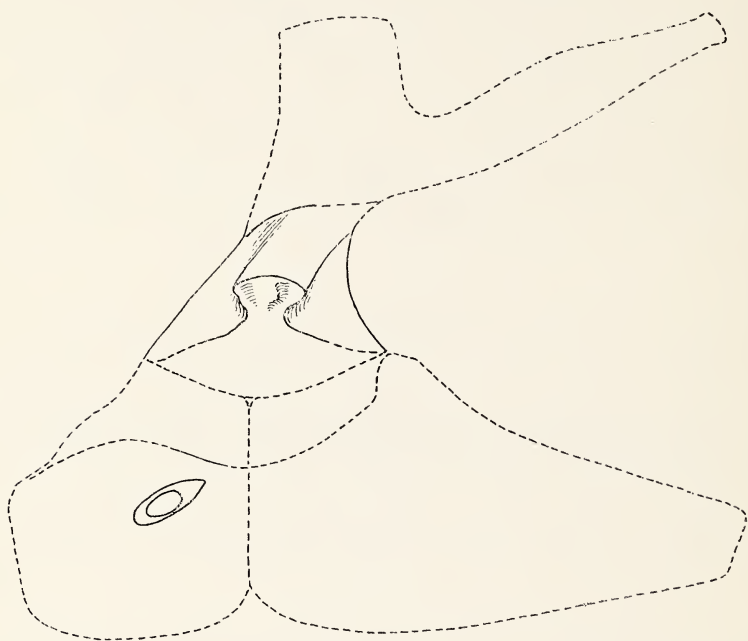


Fig. 11. cf. *Mauchchunkia bassa* Hotton, NMNH 26369. Pelvic girdle, left lateral aspect, restored after *Archeria*, $\times \frac{3}{4}$.

Humerus: Only the head of the humerus is included in the holotype of *Mauchchunkia*. In dorsal aspect, it appears as a gently rounded, relatively featureless knob that is strongly flattened in a dorso-ventral plane. Its proximal end is largely unfinished and was capped by cartilage in life. Posteriorly the unfinished area spreads onto the dorsal surface of the humerus (fig. 12A, LD), and around its margin the finished bone is produced into a marked rim. This is evidently the insertion of the latissimus dorsi muscle; it is larger and more distinct than the same region of *Archeria*, more nearly comparable to the l. dorsi insertion of pelycosaurs.

The exact shape of the proximal articular surface is undeterminable. However, the proximal end of the humerus is appreciably thickest at its midpoint, as though the articular surface turned obliquely around the end from an anterodorsal to a posteroventral point as in primitive tetrapods generally, in contrast to the strap-shaped proximal articulation of the humerus of *Archeria* as restored by Romer (1957). The unfinished surface extends anteriorly along the proximal end of the bone almost to the deltopectoral crest, from which it is separated by about 5 mm of finished bone.

The remainder of the humerus, and the front limb described below, are based entirely upon material catalogued as NMNH 26368. Although the association between this material and the holotype of *Mauchchunkia* is not absolutely certain, and the front limb so reconstructed is a composite, the results are self-consistent and are consonant with the general structure of *Mauchchunkia*.

The deltopectoral crest (fig. 12B, DP) is a stout, prominent process that extends about one-third of the way distally along the ventral surface of the humerus. Its face is unfinished and very broad. In shape it resembles that of the sphenacodont pelycosaurs much more closely than it does the poorly developed deltopectoral crest of *Archeria*, but the unfinished face is directed more anteriorly than ventrally as in pelycosaurs. Except for the deltopectoral crest the ventral surface of the humerus is flat and featureless.

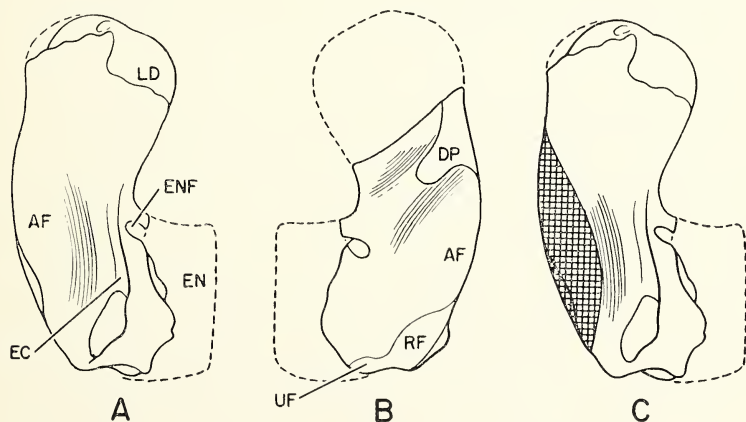


Fig. 12. *Mauchchunkia bassa* Hotton, NMNH 22573, and cf. *M. bassa*, NMNH 26368. Left humerus, composite. A, dorsal aspect; B, ventral aspect; C, dorsal aspect with anterior flange blocked out; all in plane of proximal end. Key to processes: AF, anterodorsal flange; DP, deltopectoral crest; EC, ectepicondyle; EN, entepicondyle; ENF, entepicondylar foramen; RF, radial articular facet; UF, ulnar articular facet, $\times \frac{3}{4}$.

In dorsal aspect (fig. 12A) the humerus resembles that of *Archeria* more closely than it does the humerus of other early tetrapods. As in *Archeria*, the basic tetrahedral pattern is obscured by the large size and quadrate shape of the entepicondyle, and by the development of a broad flange lateroanterior to the ectepicondyle.

The posterior margin of the humerus is pierced by a clearly defined entepicondylar foramen (fig. 12A, ENF) about halfway along its length. The foramen slants in a distal direction from the dorsal to the ventral surface, and lies very close to the proximal root of the entepicondyle, as in *Archeria*. These relationships are preserved in the left humerus of NMNH 26368, in which, despite extensive destruction of the entepicondyle, a short spur of bone projects to the rear, just proximal to the remains of the entepicondylar foramen. This little spur of bone also demonstrates conclusively that the proximal margin of the entepicondyle turns backward to form a right angle with the axis of the humerus. Thus we can be certain that the entepicondyle of *Mauchchunkia* has the same broad, flat, quadrate appearance as that of *Archeria*. How broad it was cannot be determined, but the broken medial edge is very thick, which suggests that the entepicondyle was prominent.

The ectepicondyle is a tall, narrow ridge, the crest of which is smoothly rounded (fig. 12A, EC). It is most prominently developed at its distal end and tapers gradually in a proximal direction for about two-thirds the length of the humerus. Distally it overhangs the unfinished radial articulation; its unfinished distal end is separated from the radial articulation by about 4 mm of finished surface.

The distal articular faces of the humerus are preserved only as areas of unfinished bone. Their margins are very distinct, for the finished bone that delimits them is produced into a fine rim, as it is around the margins of the latissimus dorsi insertion. Although the radial and ulnar surfaces are confluent, they can be distinguished easily. The radial articulation lies below the distal end of the ectepicondyle. Its surface is extensive; a small part faces distally as in *Archeria*, but a much larger part spreads onto the ventral surface of the humerus and faces downward (fig. 12B, RF), in contrast to the arrangement in *Archeria*. The actual articular surface must have been convex because it lay upon both distal and ventral surfaces, but if it were restored to resemble the radial articulation of pelycosaurs, it would have to be a huge ball composed almost entirely of cartilage. It is more likely that the cartilage cap was relatively thin, so that the greatest convexity of the articular surface occurred where it curved from the distal to the ventral surface of

the humerus, and that the large ventral part was only gently convex. The articular surface for the ulna lies at the distal root of the entepicondyle and faces distally (fig. 12B, UF).

The humerus is thickened along its axis, in a zone running from the ulnar articular facet at the distal end, through the base of the deltopectoral crest, to the middle of the humeral head. The ends of the bone are "twisted" on the axis to form an angle of about 45° between the planes of the distal and proximal articulations, a value closely comparable to that of terrestrial tetrapods and in marked contrast to the 20° to 25° for this angle in *Archeria*, cited by Romer (1957). This comparison reinforces the possibility that the proximal articulation was more obliquely placed than in *Archeria*.

The broad flange of bone produced anteriorly below the ectepicondyle is proportionately larger in *Mauchchunkia* than in *Archeria* (fig. 12A and B, AF). It arises proximally from the anterior surface of the deltopectoral crest and passes distally to fade into the base of the ectepicondyle. Proximally it lies in the same plane as the head of the humerus and distally it lies in the same plane as the distal articular surface; as a consequence it presents a distinctly undulant surface because of the high angle between the ends of the humerus.

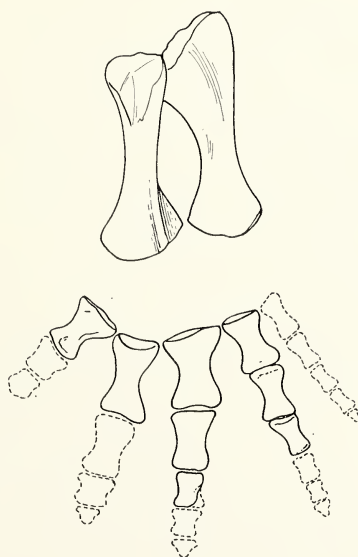


Fig. 13. cf. *Mauchchunkia bassa* Hotton, NMNH 26368. Left forearm and hand, extensor aspect, position of elements restored, $\times \frac{3}{4}$.

Radius: The radius is cylindrical, rather stouter in proportion to its length than the radius of *Archeria* but otherwise very similar to it. Its proximal articular facet is circular in outline and the surface is almost flat, except for a shallow trough whose transverse orientation corresponds to the plane of the distal articular surface of the humerus. The distal articular surface of the radius is roughly the shape of an isosceles triangle, its apex being directed medially. Extensor and flexor surfaces are essentially smooth. On the lateral surface there is a fine arcuate line of rugosity occupying the distal two-thirds of the bone, curving from the extensor to the flexor surface, which may mark the attachment of an interosseous membrane. Along the medial side there is a low, sharp-edged ridge developed over most of the length of the bone, which probably marks the medial boundary between extensor and flexor surfaces. The ridge becomes more prominent at its proximal end, which is unfinished and may mark the attachment of a biceps tendon.

Ulna: The ulna of *Mauchchunkia* is similar in all respects to that of *Archeria*, except that like the radius it is somewhat stouter in proportion to its length. Although the tip of the olecranon process is not preserved because it was not ossified, the proximal articular surface is obviously concave and faces medioproximally.

Elbow joint: The articulating surfaces of the ulno-humeral joint are of standard tetrapod pattern, and the joint evidently functions as a simple hinge, the ulna turning through an arc of about 90° . The radio-humeral joint also allows an arc of about 90° , because the humeral facet for the radius passes from the distal to the ventral surface of the humerus. As a consequence the forearm can turn, relative to the humerus, from a straight-line orientation in full extension to a right-angle orientation in full flexion.

In the functional position of the limb during locomotion, the humerus is oriented horizontally in such a way that the larger portion of the radial articular facet faces downward, and the forearm is fully flexed. In this position the radius stands vertically, with the large ventral moiety of the radial articular facet of the humerus resting on top of it. The radius is thus a weight-bearing column, for which its short, stocky form is well adapted.

In its flatness, the radial component of the radio-humeral joint of *Mauchchunkia* resembles the weight-bearing tibial component of the knee of higher tetrapods. The flat surface of the radius is matched incongruently to the convex surface of the humerus in the elbow of *Mauchchunkia*, much as the flat tibial surface is matched to the convex distal end of the femur in higher forms. Both of these

joints are anatomically unstable because of incongruence; stability is established in the elbow of *Mauchchunkia* by the congruent bearing surfaces of the ulno-humeral joint, and in the knee of higher tetrapods by tendons and ligaments crossing the joint. The radio-humeral joint of *Mauchchunkia* thus bears a closer resemblance to the knee than to the elbow joint of higher tetrapods, and like the mammalian knee appears to be a weight-bearer that must move through a wide angle in a single plane.

The similarity of the radio-humeral joint to the knee of higher tetrapods suggests that pronation and supination were of little functional significance in the elbow of *Mauchchunkia*. Such rotation of the radius as occurred during locomotion would have had about the same magnitude and function as the rotation of the tibia on the femur that takes place during flexion and extension of the knee in generalized mammals.

Hand: Except for those elements here restored as third metacarpal and proximal phalanx (fig. 13), all of the elements of the hand were disarticulated, and all were most closely associated with the left humerus. Little detail can be added to what is shown in figure 13, which indicates primarily that the hand of *Mauchchunkia*, like the rest of the front limb, was large and stout in proportion to the size of the animal, considerably more so than the front limb of *Archeria*.

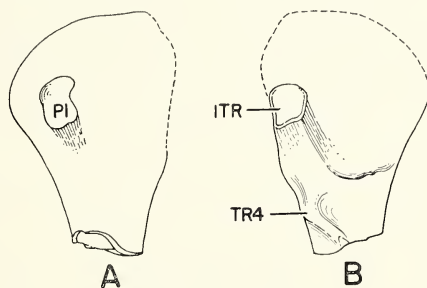


Fig. 14. cf. *Mauchchunkia bassa* Hotton, NMNH 26369. Right femur. A, dorsal aspect; B, ventral aspect. Key to processes: ITR, internal trochanter; PI, insertion of puboischiofemoralis or ischiotrochanteric muscle, or both; TR 4, fourth trochanter, $\times \frac{3}{4}$.

Femur: The heads of the right and left femora associated with NMNH 26369 are nearly as broad as the femur of *Archeria* illustrated by Romer (1957, fig. 8C), but the shafts taper to about one-third the width of the femoral shaft of *Archeria*. Some of the broadening of the femoral head of *Mauchchunkia* may be the result of distortion after burial, but the femur does seem to be proportionately larger and slimmer than that of *Archeria*.

The distance from the internal trochanter to the proximal end of the femur is approximately twice that of *Archeria*, indicating a much higher degree of ossification. The shape of the articular surface cannot be determined because the proximal end of the bone is covered by fragments of pubis. The unfinished surface that occupies most of the proximal end of the femur narrows abruptly anteriorly. It is separated from the unfinished end of the internal trochanter by a sharp ridge of finished bone about 5 mm long.

The unfinished end of the internal trochanter is similar in shape to that of *Archeria*, being short and broad rather than long and narrow as in pelycosaurs. The entire internal trochanter, including the unfinished end, is much more prominent than in *Archeria*. The anterior wall of the intertrochanteric fossa is well developed, being formed chiefly by the internal trochanter, but the posterior wall is poorly defined.

The fourth trochanter is very prominent. Proximally it consists of an area of marked rugosity lying at the root of the internal trochanter, and as it curves distally and posteriorly toward the middle of the ventral surface of the shaft it becomes narrow, and is produced into a high, sharp ridge. It passes insensibly into the adductor ridge, which continues down the shaft of the femur with no evident diminution in height as far as preserved.

Dorsally the head of the femur is gently convex. It is nearly featureless except for a well-defined patch of unfinished bone at the proximal end of a low swelling near the posterior margin. This area probably represents the confluent insertions of the ischiotrochantericus and puboischiofemoralis internus muscles (cf. Romer and Price, 1940, fig. 35). The dorsal surface is marked along its proximal margin by minor rugosity and fluting, the latter oriented more or less radial to the margin; such sculpture may mark the site of attachment of a joint capsule.

DISCUSSION

Mauchchunkia is a remarkable tetrapod, first because of its extreme primitiveness, which coincides happily with its great geologic age, and second because terrestrial adaptations can be identified in many aspects of its structure. It is short-coupled and stout-limbed like *Ichthyostega*, which confirms the idea, suggested by Panchen (1966) and elaborated by Carroll (1969), that terrestrial adaptation was fundamental to the structure of the earliest tetrapods. But the retention of a fish-like tail fin in *Ichthyostega* and the evidence of aquatic larval stages in a variety of reptiliomorph anhracosaur shows that these animals were not completely free of

water. Rather, their body and limb proportions suggest that they were primarily walkers and waders of rather turtlelike habit, to be contrasted with the long-bodied, short-limbed, swimming embolomeres and the flattened, bottom-dwelling, persistently aquatic temnospondyles.

Another anthracosaur from Greer, *Proterogyrinus* (Romer, 1970), is also primitive but is much closer than its contemporary *Mauchchunkia* to true embolomeres; comparison with this animal suggests that *Mauchchunkia* illustrates both the organization of a basic anthracosaur stock and the stem from which arose the reptiliomorph tetrapods, including gephyrostegids, seymouriamorphs, and true reptiles. Some reptiliomorph tetrapods, such as *Seymouria* and the early pelycosaurs, seem to have had much the same habits as *Mauchchunkia* and *Ichthyostega*, while others, such as the gephyrostegids and the earliest captorhinomorphs, may have been more terrestrial, attaining a mode of life comparable to that of terrestrial salamanders or lizards. These differences in habit seem to be correlated with size, for *Ichthyostega*, *Mauchchunkia*, the earliest pelycosaurs, and *Seymouria* were all of moderate size; the embolomeres and bottom-dwelling temnospondyles tended to become very large, while the gephyrostegids and captorhinomorphs were very small (less than half the size of *Mauchchunkia*). The origin of various lines of early tetrapods, including the first reptiles, appears to have been a matter of adaptive radiation controlled primarily by the degree of dependence upon standing water, and a detailed comparison of *Mauchchunkia* with *Proterogyrinus* on the one hand, and with more advanced reptiliomorph tetrapods on the other, affords many data for conjecture about these origins.

Primitive characters and terrestrial adaptation: The primitiveness of *Mauchchunkia* is indicated, more or less independently of terrestrial adaptation, by the length of skull table and postparietal bone (cf. Westoll, 1943), in which *Mauchchunkia* is more closely comparable than any other anthracosaur to *Ichthyostega*, and by its ventrally located, wedge-shaped or crescentic intercentra, in which it resembles *Ichthyostega* and certain rhipidistian fishes (cf. Romer, 1947, 1964). The crescentic shape of the intercentra probably represents a definitive adult condition in *Mauchchunkia* rather than an ontogenetic stage in the development of a more conventional embolomeric vertebral pattern, for the high degree of ossification of other vertebral elements and the completeness of the skull bones in the holotype indicate that the individual was essentially mature when it died.

The inclusion of a part of the supratemporal in the dorsal mar-

gin of the otic notch may also be a primitive character, although in this respect the otic notch of *Mauchchunkia* resembles that of the reptiliomorph anthracosaurs more closely than the otic notch of embolomeres. In the traditional view of the origin of the amphibian otic notch from the spiracular cleft of fishes, it is logical to suppose that the short embolomere notch, with its dorsal margin restricted to the tabular, is more primitive than the longer one of *Mauchchunkia*. But because the anthracosaur otic notch originated in relation to a persistent hinge between skull table and cheek, it is equally likely to have been elongate or ill-defined anteriorly at some primitive stage, which may well be illustrated by *Mauchchunkia*.

The large size and quadrate shape of the humeral entepicondyle (fig. 12, EN), and the flange of bone produced anteriorly from the shaft of the humerus (fig. 12, AF), are probably conservative features, perhaps held over from a fishlike stage, for they are retained until the early Permian in the aquatic embolomere *Archeria*, in which they are associated with small limbs and weak muscle attachments. In *Mauchchunkia*, however, they are associated with relatively large limbs and powerful muscle attachments. The entepicondyle of the pelycosaur *Ophiacodon* is proportionately smaller than that of *Mauchchunkia* but retains something of the quadrate shape, which only disappears in more advanced pelycosaurs as the proximal half of the humerus increases in length. The anterior flange contributes to the exotic appearance of the humerus of *Mauchchunkia*, but its deletion (fig. 12C) clarifies the basic similarity of the humerus to that of a primitive pelycosaur.

The similarity of development of the deltopectoral crest and the latissimus dorsi insertion to that of pelycosaurs is convincing evidence of terrestrial adaptation. The deltopectoral crest marks the insertion of large and powerful muscles that maintained the humerus in a horizontal position, supporting the body clear of the ground during locomotion on land. The same muscles also provided most of the force for flexion, adduction, and clockwise rotation of the front limb, which collectively constituted the "power stroke" in walking. The latissimus dorsi was an essential synergist of these muscles and must have been correspondingly large and powerful.

Romer (1957) has related the low angle between the planes of the proximal and distal ends, or "twist", of the humerus of *Archeria* to a primarily swimming mode of locomotion in that genus. Contrariwise, the high "twist" characteristic of *Mauchchunkia* is of the same magnitude as that of terrestrial tetrapods of the Paleozoic, and is correlated with highly developed muscle insertions in a complex of terrestrial adaptation.

TABLE 1

Lengths of front limbs are expressed in terms of Romer's orthometric linear units (Romer and Price, 1940): $OLU = r^{2/3}$, when r = transverse radius of the pleurocentrum. OLU values are listed as indices of gross size. Key to abbreviations: HS/LV, height of neural spine/length, pre- to postzygapophysis, dorsal vertebrae; LR/LH, length of radius/length of humerus; OLU, orthometric linear units, measurements in millimeters. Data sources: *Eogyrinus*, Panchen, 1966; *Archeria*, *Gephyrostegus*, Carroll, 1970; *Seymouria*, NMNH 21902; *Proterogyrinus* (estimated from figures), Romer, 1970; *Mauchchunkia*, NMNH 22573, 26368; all pelycosaurs, Romer and Price, 1940.

	No. of presacral vertebrae	OLU	Length, front limb	LR/LH	HS/LV
Embolomeres					
<i>Eogyrinus</i>	40	8.30	—	—	.66
<i>Archeria</i>	40	5.00	20	.54	.83
<i>Seymouria</i>	24	3.55	28	.65	—
<i>Gephyrostegus</i>	24	1.84	23	.53	.75
<i>Proterogyrinus</i>	—	3.90	12	.60	.90
<i>Mauchchunkia</i>	28 (max.)	3.97	24	.50	1.39
<i>Varanosaurus acutirostris</i>	27	3.66	34	.70	—
<i>Ophiacodon navajovicus</i>	27	3.83	46	.77	—
<i>O. mirus</i>	27	4.48	40	.74	—
<i>O. retroversus</i>	27	5.95	41	.78	2.00
<i>Dimetrodon limbatus</i>	27	5.53	56	.87	—
<i>Stereophallodon</i>	27	6.08	—	—	1.25

In relative length of the front limb (table 1), *Mauchchunkia* appears to fall, together with *Gephyrostegus*, about halfway between *Archeria* and the terrestrially-adapted *Seymouria*. However, this should not be interpreted without further consideration as a morphological "halfway" stage, for as has been repeatedly noted (Olson, 1951; Romer, 1957; Panchen, 1966), the basic assumption of Romer's use of orthometric linear units, that the radius of dorsal vertebral centra provides an index of body mass, may be grossly misleading in comparing animals of different habitus and distant phyletic relationship. The centra of an evolved aquatic form like

Archeria may have been smaller in proportion to body mass than those of evolved terrestrial forms like *Seymouria* or the pelycosaurs, because *Archeria* could rely upon the supportive effect of the circumambient water in which it lived, while terrestrial forms required anatomical reinforcement of the column for support on land. On the other hand, the centra of such primitive terrestrial forms as *Mauchchunkia* and *Gephyrostegus* may have been proportionately larger than those of more advanced forms, because the need for support in a terrestrial environment was probably met initially by the crude expedient of increase in size, in contrast to a more sophisticated system of articulation developed in later terrestrial animals.

To the extent that these possibilities are valid, Romer's procedure gives an excessively high value for the limb proportion of *Archeria* and an excessively low one for that of primitive terrestrial forms, in comparison with evolved terrestrial tetrapods. Such discrepancies cannot be dealt with by the procedure itself, but they can be compensated for non-numerically by downgrading the nominal value for *Archeria* and upgrading it for *Mauchchunkia* and *Gephyrostegus*. Downgrading the nominal value for *Archeria* increases the scale of difference in limb proportion between *Archeria* and the demonstrably terrestrial tetrapods, and upgrading it for *Mauchchunkia* and *Gephyrostegus* moves those genera further up the scale toward *Seymouria* and the pelycosaurs than their nominal halfway point. It is therefore evident that in proportion of the front limb, *Mauchchunkia* is considerably closer to *Seymouria* and the pelycosaurs than it is to *Archeria*.

The shortness of the radius, relative to length of humerus, is probably a manifestation of primitiveness in *Mauchchunkia*, for the morphological sequence *Mauchchunkia*-*Gephyrostegus*-*Seymouria*, which reflects general evolutionary advance correlated with time in a series of approximately common habitus, shows a consistent increase in the relative length of the distal segment of the front limb. The pelycosaurs exhibit still greater length of the distal segment; though they are contemporaneous with *Seymouria* and probably of somewhat different habitus, it is generally agreed that they represent a more advanced evolutionary condition.

The initial shortness of the distal segment of the front limb may express an early stage in the development of weight-bearing function, in probable correlation with the primitively weight-bearing nature of the elbow joint in which pronation and supination were not yet clearly defined (cf. p. 24). By contrast, the greater length of the pelycosaur radius and ulna is correlated with development of a ball-shaped radial condyle of the humerus, similar to that of more evolved tetrapods in which a greater range of pronation and

supination is possible. Lengthening of the distal segment probably occurred as a means of increasing the length of stride, which was selectively advantageous in a terrestrial environment, and it appears that development of pronation and supination accompanied this advance as front limb motion became more complex.

The combination of primitiveness and terrestrial adaptation, noted in the anatomical complex of stout limbs and short presacral vertebral column, is also reflected in the basic structure and height of the dorsal neural spines of *Mauchchunkia*. Basic structure is probably primitive because it is similar to that of embolomeres on the one hand and to that of pelycosaur on the other, and contrasts with the structure of advanced Permian seymouriamorphs and captorhinomorphs. The remarkable height of the spines in *Mauchchunkia* indicates massive development of the dorsal axial musculature, which functioned in concert with intercostal and belly musculature to lend dynamic stability to the vertebral column. The very massiveness of the dorsal musculature suggests that the column was being stabilized under terrestrial rather than aquatic conditions. Since stabilization of the column by means of muscular tension would subject the centra to compressional forces, it is probable that the high degree of ossification of the pleurocentra is associated with emphasis on the dorsal axial musculature in the general terrestrial adaptation of the vertebral column.

The atlas-axis complex is very generalized, but the atlantal intercentrum and the large, hatchet-shaped axial neural spine are both pelycosaurlike, the axial spine reflecting the former presence of a well-developed nuchal ligament. These structures appear to be adapted to support of the heavy head in a terrestrial environment, and the distinctive if minor specialization of the four postaxial neural spines indicate differentiation of a neck, signifying that considerable movement of the head was possible.

Anthracosaur phylogeny: Associated with the primitive ground plan of *Mauchchunkia*, but not particularly attributable to terrestrial adaptation, are the features by which the genus is diagnosed as a member of the Anthracosauria: tropitrahic skull; pattern and sculpture of dermal skull bones; tabular horns; and pattern of palate, dermal pectoral girdle, and neural arches. These features are for the most part characteristic of the later embolomeres, but their presence in *Mauchchunkia* suggests that they are also part of the original anthracosaur heritage. They have been variously modified in later terrestrially adapted anthracosaurs, and in the embolomeres by elongation of the snout and presacral column. *Mauchchunkia* obviously lies near the ancestry of both types, and for fur-

ther assessment of its phylogenetic significance we must refer now to its contemporary *Proterogyrinus*.

Proterogyrinus is much closer to true embolomeres in skull proportion, for the skull table is only about half the length of the face, and the contribution of the postparietal to the skull table is smaller than in *Mauchchunkia*, being roughly comparable to that of "*Paleogyrinus*" (cf. Panchen, 1964). The otic notch is short, its dorsal margin being restricted to the large tabular. The snout shows some elongation. Length of the presacral column is unknown, but the neural spines are more closely comparable in height to those of embolomeres than to the spines of *Mauchchunkia* (table 1). Spine height and length of snout suggest that the column may have been elongate, in correlation with the aquatic, piscivorous habit typical of embolomeres. Romer interprets the central elements as subequal in height and very similar in appearance; in this feature also *Proterogyrinus* resembles the embolomeres more closely than does *Mauchchunkia*. But pleurocentra as well as intercentra are described as thin hoops of bone, unossified dorsally; in anterior aspect both elements are U-shaped. Romer notes that although the type of *Proterogyrinus* was probably not mature at death, maturity would not have brought vertebral ossification to a point comparable to that of true embolomeres, and therefore places *Proterogyrinus* in a distinct family, morphologically antecedent to embolomeric forms. Its proximity to true embolomeres is indicated not only by skull structure, but also by the probability that only a genetically simple increase in rate of ossification was necessary for its vertebrae to become fully embolomeric, and it is very probably an actual ancestor of definitive embolomeres.

The vertebrae of both Greer anthracosaurs are derivable from a schizomeric pattern (Romer, 1964) in which the pleurocentrum consisted of laterally placed half-rings and the intercentrum was a ventrally located crescentic element. The vertebrae of *Mauchchunkia* conform in general to Romer's diplomeric pattern, in which the pleurocentrum is a complete perichordal ring derived by dorsal and ventral coossification of schizomeric half-rings, with the intercentrum remaining essentially unmodified. Most of the pleurocentra are advanced beyond a strictly diplomeric condition because they are ossified into complete discs, but a trace of schizomeric structure is retained in the atlantal pleurocentrum, in which dorsal and ventral marginal notches (fig. 8B) suggest that the element was formed by the fusion of lateral halves. The vertebrae of *Proterogyrinus* are not diplomeric; the pleurocentrum seems to be formed simply by coossification of schizomeric half-rings below the notochord, and the intercentrum by dorsal ossification of the horns of the original crescent. To distinguish these divergent pat-

terns in terms of their theoretical origins, the vertebrae of *Proterogyrinus* are styled "neoschizomerous" and those of *Mauchchunkia* "neodiplomerous".

The neoschizomerous vertebral pattern of *Proterogyrinus* is a virtually ideal morphological intermediate between schizomerous and embolomerous stages, and indicates that embolomerous vertebrae originated directly from a schizomerous ancestral pattern without going through a diplomerous stage at all. This, as Romer (1970) notes, invalidates his earlier view (Romer, 1964) of the diplomerous pattern as intermediate between schizomerous and embolomerous stages. Moreover, it seems probable that the neodiplomerous structure of *Mauchchunkia* evolved from a schizomerous antecedent during the same period of time that the neoschizomerous pattern of *Proterogyrinus* was being developed. Thus the origin of the vertebral patterns of *Mauchchunkia* and *Proterogyrinus* must be attributed to independent trends that diverged from the level of a putative schizomerous common ancestor a short time before the Upper Mississippian. The possibility, suggested by Carroll (1970) for *Gephyrostegus*, that neodiplomerous intercentra may have become completely ossified dorsally in very old individuals, is not known in actuality and in any case is probably not phylogenetically significant.

Exclusion of diplomerous and neodiplomerous structure from the line of embolomere descent greatly enhances the significance of these patterns as indicators of the stem from which reptiliomorph tetrapods sprang, which establishes *Mauchchunkia* as the earliest known member of that stem, just as *Proterogyrinus* is the earliest known member of the line that led to embolomeres. Assuming an origin from schizomerous antecedents, the divergent trends in the two lines may be interpreted in terms of ontogenetic acceleration in the rate of ossification of vertebral centra, which in the line of *Mauchchunkia* was rapid but affected primarily the pleurocentrum, leaving the intercentrum little changed. In the descendants of *Mauchchunkia*, ossification of the intercentrum was de-emphasized and the element eventually disappeared. In the line of *Proterogyrinus*, acceleration of the rate of ossification was slower, but affected pleurocentrum and intercentrum alike, leading ultimately to complete ossification of both elements in the definitive embolomeres.

Since the terrestrial adaptations of *Mauchchunkia* appear to be for the most part conservative in nature, establishment of diplomerous structure in that line probably represents a refinement of the originally terrestrially oriented organization of the basic stock. Emphasis on the pleurocentrum probably arose with emphasis on the dorsal axial musculature as a means of stabilizing the column

in a terrestrial environment, in response to selective pressure exerted by the need for support inherent in such circumstances.

The origin of an embolomere stock, on the other hand, was probably initiated as the ancestors of *Proterogyrinus* found themselves able to exploit a more completely aquatic mode of life. The less well-ossified condition of the centra of *Proterogyrinus* indicates that selective pressure occasioned by the need for support was not as effective in the ancestry of *Proterogyrinus* as in that of *Mauchchunkia*, as would be expected if the former had taken to living consistently in deeper water. Instead of requiring refinement of structures utilized for support, the aquatic environment exerted pressure toward improvement of a swimming habit, to which the embolomere line responded by elongation of the column in the development of a sinuous swimming motion. The selective advantage of elongation of the column was presumably the increased flexibility it afforded. If, as Panchen (1966) suggests, the pleurocentrum and intercentrum of the same segment were movable on each other, coeval ossification of the two elements would also enhance flexibility without appreciable sacrifice of strength, and hence could result from the same selective forces that produced column elongation.

Whether elongation of the column preceded complete ossification of the central elements or was concurrent with it cannot be determined without a presacral vertebral count for *Proterogyrinus*. In any case, by the early Pennsylvanian the embolomeres were elongate swimmers with fully ossified central elements, and many of them were quite large. Like most early tetrapods, these animals were predaceous, and their increase in size from the Mississippian to the Pennsylvanian was probably selected for as a consequence of competition with predaceous fish. The utilization of sinuous motion by large swimming predators may have subjected the individual components of an elongate column to unusual compressional and tensional stresses, another factor that would select for complete and coeval ossification of pleurocentrum and intercentrum.

Origin of reptiles: Although *Mauchchunkia* is clearly a member of the reptiliomorph stem, as a generalized anthracosaur it exhibits no closer morphological affinity to one reptiliomorph branch than to another, and since it occurs nearly a full period earlier than any, it represents a group that must have included the ancestors of gephyrostegids, true reptiles, and seymouriamorphs alike. Members of this group, which were primarily walkers and waders that lived in shallow ponds and streams and along the margins of deeper bodies of fresh water, were as generalized in habit as they were

in structure, and provide an excellent starting point for the consideration of the origin of reptiles as an adaptive radiation.

The earliest tetrapods to occupy environments more highly terrestrial than the margins of standing water were all very small (Carroll, 1969), the largest of them less than half the size of *Mauchchunkia*. As examples Carroll cites the gephyrostegids and captorhinomorphs of the Middle Pennsylvanian, but notes also (written communication, 1970) that some of the earliest pelycosaurs on record, which date from the same time, are the same size as gephyrostegids and primitive captorhinomorphs. He suggests that the success of these animals under terrestrial conditions stemmed from advantages conferred by small size, which mitigated problems of support and enabled the animals to utilize secretive behavior to conserve water, and which ultimately proved decisive in the origin of the amniote egg. At a preamniote level, small size would reduce the need for the egg to be laid in standing water because of reduced need for support, greater facility for respiration, and the sufficiency of local dampness to keep a small egg moist. Subsequent steps in the evolution of the amniote egg required development of direct internal fertilization and a large-yolked egg in which the larval stage could be passed. Evolution of living amphibians provides plausible parallels for this phase, for such features have appeared independently a number of times in connection with increasing terrestriality. Noble (1931) points out that both direct internal fertilization and large-yolked eggs are characteristic of the relatively archaic caecelians, and implies that these features may have been generally present in early tetrapods.

Carroll envisions the amniote egg as having originated in a line of small progressive forms such as gephyrostegids, which, having become highly terrestrial as adults, began to lay their tiny eggs in damp places on land as do the living plethodont salamanders, and later evolved direct internal fertilization and a large-yolked egg. He implies that the final stages in the evolution of amnionic structure took place during the transition from gephyrostegids to captorhinomorphs, and for the transition itself he presents a convincing morphological argument. Uniformity of egg structure among living amniotes indicates strongly that all are derived from a single type, which in turn means either that the amniote egg arose only once or that any other form that approximately duplicated amnionic structure became extinct without issue.

Since the reasons for considering captorhinomorphs to be amniotes apply as well to pelycosaurs, it follows from the argument for a single origin of the amniote egg that one group must have been derived from the other. But though pelycosaur and captorhino-

morph lines converge when traced backward from the Permian, they are still distinct at the earliest appearance of reptiles in the Middle Pennsylvanian. The possibility must therefore be admitted that pelycosaurs arose from an anthracosaur level independently of the origin of captorhinomorphs; they may have come from gephyrostegids, or perhaps even from animals of a mauchchunkiid level of organization.

Such an eventuality demands examination of alternative possibilities for the origin of the amniote egg. As a first step, two factors must be noted: one, that a large-yolked egg may well have been characteristic of a variety of primitive tetrapods as an inheritance from the archaic fishes from which they sprang; and two, that seasonal water fouling and drying were probably characteristic of the bodies of water in which members of the conservative anthracosaur line lived. A large-yolked, sizeable egg would predispose its possessors to pass their larval stages within the egg in any circumstances that were inimical to free larval life. The larger the egg, the more vulnerable it would be to asphyxiation in oxygen-poor surroundings because of the ratio of surface to volume, but by the same token, the less vulnerable it would be to desiccation. In these respects a large-yolked egg of appreciable size is well integrated with the terrestrially oriented morphology of the earliest anthracosaurs.

It is entirely conceivable that primitive tetrapods like *Mauchchunkia*, having established themselves in pond and river margin environments as walkers, waders, and paddlers, would tend to utilize the extreme margins or the damp banks of these bodies of water as places in which to lay their eggs. This habit would be immediately advantageous, for eggs laid in such places would be at least partially exposed to air and so would be more likely to survive the effects of water fouling. Quite possibly they would also be less subject to predation. At the same time they would be subject to desiccation, which they were predisposed to resist, but which would introduce the same major selective factor that was operative on the eggs of gephyrostegids and primitive captorhinomorphs that were deposited in more completely terrestrial surroundings.

Conditions prerequisite to the origin of the amniote egg thus probably obtained in conservative anthracosaurs of the reptiliomorph line. It is doubtful that amniotic structure as such was present as early as *Mauchchunkia*, for indications are that seymouriamorph derivatives of the mauchchunkiids went through a free-living larval stage, but the amniote egg may well have appeared before the establishment of definitive reptilian osteological structure. If this were the case, it would certainly have been a factor

in the success of the smaller forms that were making their way into more highly terrestrial environments, and in addition it would account for the presence of conservative lines such as the limnosceloids and perhaps the diadectids, which at the same time were evolving a reptilian morphology without being very small or being markedly more highly adapted to terrestrial conditions.

Alternatively, it is possible that the last stages in the establishment of amniotic structure occurred independently in small, highly terrestrial ancestors of captorhinomorphs and pelycosaurs, in more conservative ancestors of limnosceloids, and even, perhaps, in the seymouriamorph line after the establishment of *Seymouria*-like forms but before that of the family Diadectidae. This notion seems to imply that the amniote egg arose several times, and brings to mind the putative history of the later synapsid reptiles, in which a wide variety of progressive characters evolved in tightly parallel fashion under the pressure of an increasingly active mode of life. However, the anthracosaurs in question were removed but a short distance in time from their common ancestry, and must have been much more closely interrelated than were the synapsids. The greater part of the evolution of amniotic structure had already taken place in what was essentially a single line, and the selective pressure that had brought it along continued to affect the adaptive branches to which the main line gave rise. The differences by which these branches are identified foreshadow their great phylogenetic potential, but this should not lead us to exaggerate the differences among them at the time of branching, with respect to the genetic factors controlling the evolution of egg structure. Whatever finishing touches were put upon amniote structure after the branching of reptiliomorph tetrapod lines were direct consequences of their common history, and from an operational point of view the origin of the amniote egg can be regarded as single. In this light, the ease with which all reptiliomorph lines can be derived from a hypothetical group no higher than family, whose basis is the genus *Mauchchunkia*, obviates for the moment the vexed question of the polyphyletic origin of major groups of reptiles.

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THE GIRDLED ROAD SITE, AN EARLY WOODLAND HUNTING STATION IN LAKE COUNTY, OHIO

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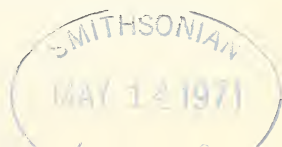
ABSTRACT

Archaeological survey of a proposed reservoir area in Cascade Valley, Lake County, Ohio, has revealed a small single-component site along the bluffs bordering Big Creek. Analyses of the recovered artifacts and the nature of their topographic and stratigraphic location indicate that the site represents a small seasonal hunting camp occupied early in the first millenium B.C.

In May, 1969, a preliminary archaeological survey of a portion of southern Lake County, Ohio, was undertaken by the author for the Cleveland Museum of Natural History. The area investigated lay within the proposed expanded boundaries of the Girdled Road Reservation of the Lake County Metropolitan Park District in Leroy and Concord townships. The proposed reservation area is bounded roughly by Winchell Road, State Route 608, and Williams Road to the west, Huntoon Road to the north, Callow Road on the east, and the Lake-Geauga county line to the south.

Topographically the area consists of a gently rolling portion of the glaciated Allegheny Plateau, dominated by the deeply incised valley of Big Creek and its tributaries, Aylworth Creek and East Creek. The latter stream represents a more juvenile (less entrenched) drainage system which appears to have been captured recently by Big Creek. East Creek presently joins Big Creek about 60 yards below the 18-foot Cascade Falls on Big Creek. This is the most steeply entrenched portion of the valley, and Big Creek flows

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LAKE ERIE

GIRDLED ROAD SITE

LAKE COUNTY

OHIO



0 1 MILE
SCALE



approximately 150 feet below the plateau surface. This is also the widest portion of the flood plain and is called Cascade Valley. It is approximately a quarter of a mile wide from the junction of East Creek for about three-quarters of a mile downstream (northwest). Two miles below this deep valley, Big Creek flows out onto the lake plain and into Grand River approximately 5 miles above the river's entrance into Lake Erie (fig. 1). This deep valley described above was the proposed site of a dammed lake, and archaeological survey was concentrated in that area.

ARCHAEOLOGICAL RECONNAISSANCE

Several days of surface collection and archaeological testing were spent in Cascade Valley itself. With the exception of randomly distributed historic artifacts from the nineteenth and twentieth centuries, no cultural material was recovered within the Cascade Valley. The steep (over 40°) banks of the valley were too denuded by sheet runoff to offer much hope of finding in situ cultural material. It was also felt that the gradient itself should have prohibited occupation. Several test-pits each measuring 5 by 5 feet were excavated on the more gentle slopes along the western side of Cascade Valley but produced no cultural material. Archaeological testing along the east rim of the valley was limited to the undisturbed southeastern portion lying north of East Creek. A total of four 5 by 5 feet test pits were excavated which produced no cultural material. On the southernmost promontory on the eastern rim, isolated on the south by East Creek and Cascade Falls and on the north by a more gentle fifty-foot ravine cut by seasonal streams, a single short-term component was encountered at a depth of 18 inches below the surface (fig. 2).

GEOMORPHOLOGY

The occupation encountered in these tests could be followed through three 5 by 5 feet excavation units where it was defined as a thin discontinuous midden deposit lying in erosional depressions on the surface of a poorly developed soil horizon (fig. 3). The underlying grayish-brown calcareous sands displayed a poorly

◆ Fig. 1. Map showing location of Girdled Road site. Star indicates site.

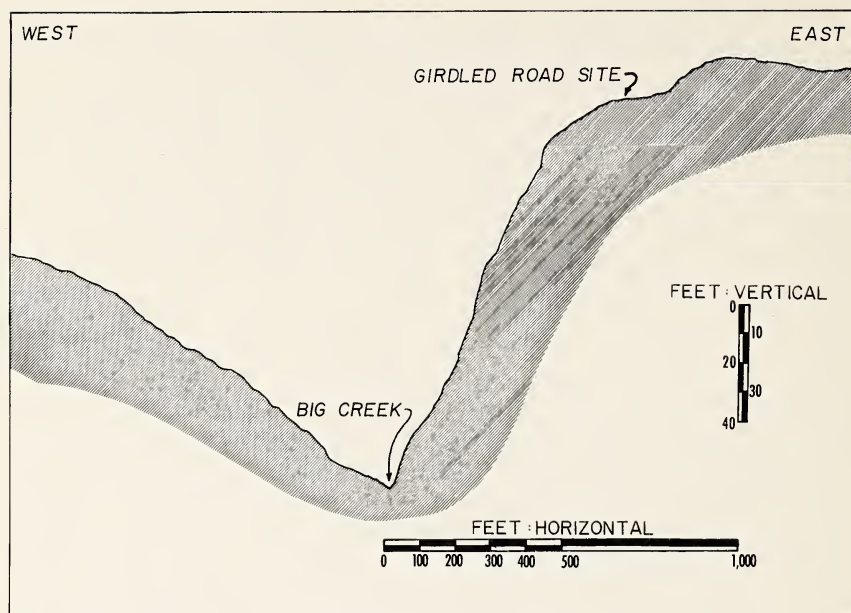


Fig. 2. Cross section of Cascade Valley traversing Girdled Road site.

sorted particle-size distribution characteristic of lacustrine deposition (Friedman, 1961, p. 514-529), probably representative of dune formation along Lake Cuyahoga about 13,000 years ago (Rau, 1969, p. 25-29). With the draining of this proglacial lake after 11,000 B.P. a period of warmer weather favored the rapid development of an "inceptisol" with a weak illuvial horizon (U. S. Soil Conservation Service, 1960). It was on this surface that the human occupation took place. Post-occupational geomorphological activity resulted in the truncation of elevated portions of the midden and burial beneath the deposition of loam eroded from further upslope. A period of lessened precipitation appears to have existed as seen in the development of a clear A_2 horizon containing fragile clay minerals (Bunting, 1965) immediately overlying the cultural materials. The present ground surface represents a historically disturbed (A_p) horizon.

The only pedological data of immediate concern are the (1:1) pH values for the soil horizon noted. The lowest (C_1) horizon has a neutral value of 6.8 while the succeeding horizons range between 4.3 and 5.7. The occupational midden itself gave pH values from

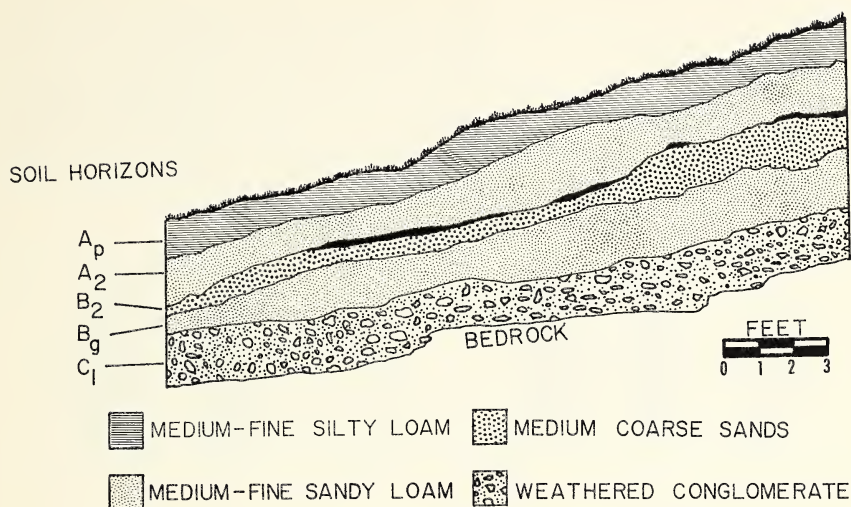


Fig. 3. Stratigraphic profile of test pits 17 and 18 excavated at Girdled Road site. Dark lenses represent cultural materials.

4.9 to 5.2. These rather acid soils clearly are a recent result of downward percolation of humic-acid-enriched rainwater (U.S. Bureau of Plant Industry, Soils and Agricultural Engineering, 1962) and have had the result of destroying most of the faunal material from this site.

CULTURAL MATERIALS

The distribution of cultural materials within the occupation area was quite disappointing. The thickness of the deposits and their lack of internal stratification indicate a single component of rather limited duration. Erosion has removed all but isolated portions of what was presumably a continuous deposit. While these diagenetic processes have rendered meaningless any attempts at analyzing the spatial distribution of the artifacts recovered, the total observed extent of the area displaying these deposits may provide some estimate of population. This point will be dealt with in the interpretive section of this report.

No features were noted at the Girdled Road site. While areal clusters of artifacts or charcoal were probably present, diagenetic erosion has removed any indications of these. Subsurface features,

however, should have been recoverable. Their absence thus confirms the suggestion of an occupation of limited duration.

Recovered artifacts consisted of three stemmed projectile points (fig. 4 A, C); two large ovate bifacial knives (fig. 4 B, D), a large bifacial sidescraper (fig. 4 E); a broken slate gorget or celt (fig. 4 F); 104 chert and flint chips; and two rolled copper beads (fig. 4 G).

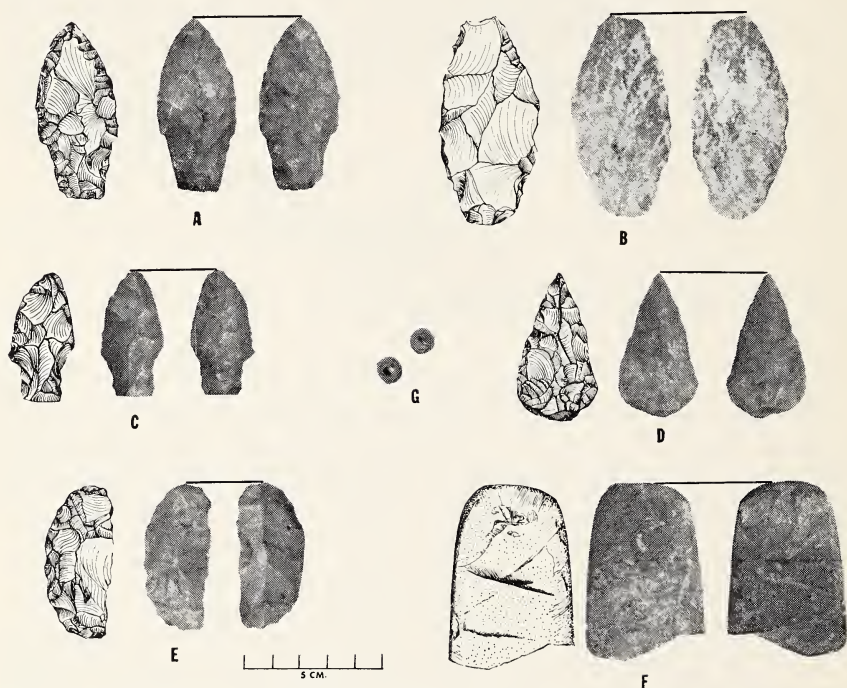


Fig. 4. Artifacts from the Girdled Road site. A, C, projectile points; B, D, bifacial blades; E, scraper; F, celt; G, rolled copper beads.

CHIPPED STONE

The chipped stone artifacts offer the best means of assigning relative temporal placement to this component. Their metric attributes are presented in table 1.

The entire lithic assemblage is typologically consistent and argues for an Early Woodland occupation. The stemmed points are morphologically and metrically analogous to the flat-based "Cresap points" which Dragoo (1963, p. 109-113) recovered from the Cresap

TABLE 1
METRIC ATTRIBUTES OF CHIPPED STONE ARTIFACTS
(In millimeters)

	Length	Width	Thickness	Haft Width	Edge Length	Raw Material
STEMMED POINTS						
	45.2	23.3	8.3	14.1	33.0	Flint Ridge Flint
	62.7	28.8	9.5	19.2	43.7	Glacial Pebble Cherts
	51.5	29.4	11.1	16.7	38.9	Devonian Outcrop Cherts
OVATE BLADES						
	52.3	29.3	9.0	—	—	Flint Ridge Flint
	73.7*	35.5	11.2	—	—	Plum Run Flint
SIDE SCRAPER						
	53.1	25.3	14.2	—	—	Flint Ridge Flint

* tip broken

Mound in West Virginia. Similar points are reported from numerous Adena Phase burial mounds throughout the upper Ohio valley (Dragoo, 1963, p. 118-121; Webb, 1942, p. 335). In northern Ohio they are associated with components of the coeval Leimbach Phase (Shane, 1967). The ovate blades from the Girdled Road site are morphologically and metrically analogous to "Adena leaf-shaped" blades or points. Such artifacts are a common type on Adena Phase sites in the Ohio valley (Dragoo, 1963, p. 107-108, Webb and Snow, 1945, p. 82) and in northern Ohio during the Leimbach Phase (Shane, 1967, p. 114-116). The large heavy sidescraper, although less useful as a horizon marker, is also a common artifact on Adena or Leimbach Phase sites throughout the state (Dragoo, 1963, p. 117-121, Shane, 1967, p. 116-117, 156, 160).

The chipping debris recovered from the Girdled Road site (table 2) appeared randomly scattered throughout the truncated midden deposit. No clusters of debitage were noted in the remaining portions of the deposit. The entire midden level was hand-screened through 3/32 inch hardware cloth and numerous small chips, often missed in conventional 1/4 inch screens, were recovered. All of the typological categories of chippage are indicative of final flaking or resharpening activities. None of the initial preparation flake categories such as cores or decortication flakes were recovered from this component (cf. Brose, 1970a).

All of the chipped stone artifacts were examined under a low power (45X) binocular microscope in an attempt to interpret their function. The three stemmed points exhibited moderate to light use on edges characterized by resolved or step-flaking. While all of these points exhibited a slight sheen or polish, this was extremely intermittent and occurred both on the flake-scar surfaces and on the interlying ridges. No evidence of use striae was observed. The ovate blades exhibited some use polish on both faces, usually confined to within 7 mm of the edge. This gloss was rather continuous, and most evident on the ridges separating flake-scars. Both ovate blades were characterized by numerous more or less parallel longitudinal striations on both faces of both edges. These striations were confined to a zone within 5 mm of the edge, extending from the tip about two-thirds of the distance along the edge of the blade. The bifacial scraper showed numerous transverse striations on the steeply retouched curved edge and faint parallel longitudinal stria-

TABLE 2
FREQUENCIES AND WEIGHTS OF LITHIC DEBITAGE
BY FLAKE TYPE AND RAW MATERIAL

FLAKE TYPE	RAW MATERIAL				TOTALS
	FLINT RIDGE FLINT	PLUM RUN FLINT	GLACIAL PEBBLE CHERTS	DEVONIAN OUTCROP CHERTS	
BIFACIAL RETOUCH FLAKES					
HARD HAMMER	10 (4.8 grams)	3 (1.5 grams)	2 (0.7 grams)	1 (0.3 grams)	16 (7.3 grams)
SOFT HAMMER	2 (7 grams)	19 (7.8 grams)	1 (4 grams)	—	22 (18.8 grams)
FLAT FLAKES					
HARD HAMMER	27 (12.8 grams)	6 (4.2 grams)	8 (2.3 grams)	7 (2.3 grams)	48 (21.6 grams)
SOFT HAMMER	7 (18.7 grams)	8 (2.2 grams)	3 (4.3 grams)	—	18 (25.2 grams)
TOTALS	46 (43.3 grams)	36 (15.7 grams)	14 (11.3 grams)	8 (2.6 grams)	104 (72.9 grams)

tions along the straight edge. Numerous areas of high-use polish were observed on both faces of this artifact.

The comparison of wear patterns observed on these artifacts with experimentally produced data (Semenov, 1964) provides the functional interpretation of these artifacts with a considerable degree of confidence. The stemmed points display evidence of use fully consistent with their functional interpretation as projectile points, probably used in mammal hunting. The ovate blades show evidence of wear characteristic of hafted knives used for cutting rather soft material which occasionally encountered a more resistant material. The bifacial scraper seems to show evidence of use characteristic of two separate functions. It appears to have been used as a hand-held scraper for hides, and as a backed hand-held knife, probably for skinning.

There is no evidence to support the contention that the ovate blades represent preforms or an earlier stage in the production of the stemmed projectile points. The ovate blades display distinct wear patterns indicating that they functioned as a finished artifact. In addition, the stemmed points display no wear patterns consistent with their earlier use as knives. The two classes thus seem to represent functionally, as well as typologically, distinct artifacts.

The entire chipped-stone complex is clearly indicative of hunting and butchering activities with occasional refurbishing of knives and projectile points but no actual tool manufacture. The analyses of raw materials utilized in artifact manufacture has lead to the recognition of four distinct sources. These sources are Flint Ridge Flint, Plum Run Flint, Devonian Outcrop Cherts, and glacially derived Pebble Cherts. The mottled gray and brown pebble cherts occur commonly in the till and outwash formations of the glaciated Allegheny Plateau region of northeastern Ohio. The Devonian Outcrop Cherts represent a variety of light tan cherts common in nodules or beds in formations pertaining to the Devonian System. Around the western end of Lake Erie such outcrops in Dundee Limestone formations are noted in Hillsdale, Lenawee, and Monroe counties in Michigan, and in the Delaware Limestones in Lucas, Ottawa, Erie, and Sandusky counties in Ohio (Brose [in press]; Stout and Schoenlaub, 1945). The Plum Run Flint, which appears to be a facies of Upper Mercer Flint, and the Flint Ridge Flints have been discussed extensively in the literature of Ohio archae-

ology. The comparison of raw materials utilized in artifact manufacture and raw materials exhibited in the chipping debris recovered from the Girdled Road site (table 3) clearly indicates that

TABLE 3
LITHIC PRODUCTION AGAINST RAW MATERIAL CATEGORIES
BY WEIGHT (in grams)

	RAW MATERIAL			
	FLINT RIDGE FLINT	PLUM RUN FLINT	GLACIAL PEBBLE CHERTS	DEVONIAN OUTCROP CHERTS
ARTIFACTS				
Observed	62.7	18.5	16.2	9.5
Expected	63.0	20.4	16.4	7.2
DEBITAGE				
Observed	43.3	15.7	11.3	2.6
Expected	43.0	13.9	11.1	4.9

$$X^2 = 2.2339; df = 3; p = .50; \phi = .0124; n = 179.8$$

there is no statistical significance to the variations observed. Given the size of the sample, the observed variations could be expected by chance alone nearly fifty times out of a hundred if only a single population were involved. The implications that the recovered chipping debris was derived from the recovered artifacts seems to be well founded. Certainly, neither all of the artifacts utilized at the site, nor all of thedebitage has been recovered. It is still quite clear that we would not expect further samples to show radically different proportions of the source materials already noted.

GROUND STONE

A single broken rectangular celt, manufactured from Bedford Shale, was also recovered from the midden deposits. The celt is 65.5 mm long, with a maximum width of 44.0 mm and a maximum thickness of 8.9 mm. Heavy transverse striations were noted on both faces of the 11.2 mm portion of working edge which remained intact, making it probable that the implement functioned more as an axe than as an adze. The strong bedding planes within the rather brittle shale make it appear unlikely that the celt was intended for woodworking. Similar rectangular celts occur occasionally throughout the Ohio area in Early Woodland contexts (Dragoo, 1963; Shane, 1967) although they are usually manufactured from igneous or metamorphic rock. Small rectangular celts of sedimentary rock are increasingly common in later periods in this region.

COPPER

Two small rolled copper beads recovered from this component have analogs in the Great Lakes-Ohio valley region from the Late Archaic (2000 B.C.) through the transition to Late Woodland (A.D. 500). Both beads are quite similar, having been manufactured by cold-hammering native copper (common throughout the Upper Great Lakes) into flat sheets, then folding and cold-hammering these sheets into more or less rectangular strips. The rectangular strips would then be wrapped about some sticklike object and cold-hammered to form an overlapping rolled copper bead. All ductility had been lost at this stage of the manufacturing process. The larger bead with an internal diameter of 2.9 mm and an external diameter of 11.1 mm had been formed of a rectangular strip which was 17.4 mm long, 7.0 mm wide, and 2.5 mm thick. The smaller bead with a finished internal diameter of 2.5 mm and an external diameter of 10.2 mm had been rolled from a rectangular strip 16.8 mm long, 6.33 mm wide, and 2.3 mm thick.

Copper beads of this type represent a common artifact form in Early Woodland sites throughout the region. They are ubiquitous on those sites in the Ohio valley identified as Adena (Dragoo, 1963, p. 121-123; Solecki, 1952, p. 370; Webb and Snow, 1945, p. 99-100; Bache and Satterthwait, 1930, p. 140). They have also been recovered from most of the major components of the coeval Leimbach Phase in northern Ohio (Shane, 1967, p. 23).

EXTERNAL CULTURAL RELATIONSHIPS

TYPOLOGY

The entire material culture assemblage from the Girdled Road site is clearly related to the Early Woodland materials within Ohio. Recently there has been an attempt made to denigrate McKernian nomenclature and to refer to archaeological manifestations in terms of phase and tradition as expounded by Caldwell (1958). In this region, Prufer and others (1965) have discussed the regional Scioto Tradition which seems to extend over the entire Great Lakes-Ohio River drainage system. Within this Tradition, Shane has distinguished two contemporary phases during the first millenium B.C.: the Adena Phase in the Ohio drainage basin, and the Leimbach Phase to the north, with the only distinction between these phases based on minor ceramic variations. A critical discussion of these taxonomic questions already exists (Fitting and Brose [in press]) and need not be repeated here. What is important is the recognition of the close relationship between these two contemporaneous phases which should probably be considered a single phase of two distinct traditions within a Scioto Co-Tradition (cf. Willey and Phillips, 1958). As Shane himself has noted, the differences are merely geographic.

Typologically, all of the Girdled Road site material can be considered characteristic of materials more generally referred to as "Adena." There are several problems with this approach, however. As Webb and Baby (1957, p. 32) noted, one of the more salient features of the Adena People on their own turf is their skill at disguising information pertaining to their settlement system. Our knowledge of Adena architecture is primarily from charnel houses. Our understanding of the role which factors of topography and geography played in the patterning of sites is largely confined to some knowledge of the location of their more elaborate ceremonial mounds. Even our conception of the material culture of the Adena People is generally restricted to grave goods. Our appreciation of the extractive economy (or economies) which supported the Adena mortuary complex is severely limited and virtually worthless in reconstructing any kind of cultural ecology. The supposition that several Kentucky rock shelters were utilized as temporary hunting camps is inferential. "What people, other than the Adena Indians, could have been in these shelters, so close to the region of Adena

permanent residence, at that period?" (Webb and Baby, 1957, p. 34).

The Early Woodland period in northern Ohio was quite obscure until the recent excavations and restudy of extant collections by Orrin C. Shane III (1967). Shane has documented a number of sites located in the south-central portion of the Lake Erie drainage basin which display clear affinities with the more southern classic Adena mounds. The type site of this Phase is the Leimbach site on the Vermilion River in Lorain County, Ohio. Here Shane excavated a large midden (estimated to represent an occupation area of more than 15,000 square feet) which varied between three and eight inches in thickness. The midden contained numerous features, one of which indicated a circular structure 40 feet in diameter. This midden contained considerable amounts of ceramics which Shane has assigned to Fayette Thick, Adena Plain, and two new types, Leimbach Thick and Leimbach Cordmarked. The Leimbach ceramics clearly are a local variation of the general Early Woodland ceramic assemblage throughout the northeast. This is the sense in which Shane defines the Leimbach Phase and a coeval Adena Phase.

One of the major contributions of Shane's Leimbach excavations is his demonstration that the number and size of features in the Early Woodland occupation implies a semipermanent small village in the settlement system. Of the three radiocarbon samples submitted, the two noncontaminated ones provide dates of 540 B.C. \pm 309 years (Shane, 1957, p. 136) thus establishing the chronological position of the site. At this same time period (as determined from ceramic affinities) Shane also recognizes several other related components on northern Ohio. The lower levels of the Mixter site in Erie County represent a hunting station contemporary with Leimbach. The earlier collections from the Burrell Fort site on French Creek in Lorain County, Ohio, were reanalyzed and a portion of the site was re-excavated by Shane to reveal an early component with material similar to the Leimbach site midden. The Seaman's Fort site on the Huron River, Erie County, Ohio, excavated since 1945 by R. Vietzen was visited by Shane in the summer of 1966. While the site was badly disturbed, Shane was able to analyze earlier collections and concluded that there was an early component at Seaman's Fort, again coeval with the Early Woodland occupation at Leimbach. He further noted (1967, p. 158) that the

site was probably functionally similar to Leimbach in that it also represented a number of seasonal semipermanent occupations. An analysis of ceramics in the Ceramic Repository at the University of Michigan Museum of Anthropology lead to the recognition of another small component of the Leimbach Phase from the Mohawk Park Rock Shelter in Geauga County, Ohio.

In addition to Shane's analyses, numerous radiocarbon dates exist for Adena burial mounds within the Ohio River drainage system. Again it should be emphasized that Adena, as this term is presently used, is certainly not a culture in spite of Shetrone's (1920) original suggestion that it represented one tribe or nation. The succeeding decades, with the collection of data in a haphazard and atheoretical manner, have done little for the Adena concept other than to make Shetrone's definition less acceptable. The "traits" of Adena may be technological or economic, but for the most part are ideological. As Griffin (1948) pointed out a quarter of a century ago, a mortuary complex is not a culture.

Adena as a mortuary complex must be separated from Adena as a settlement system and Adena as a nonmortuary style zone, the latter perhaps representing some strain of ethnic unity similar to that suggested by Shetrone. Even from preliminary analysis it is clear that the distribution of these three aspects of Adena are not coterminous.

Dragoo (1963, p. 288-297) has presented a large series of radiocarbon determinations relating to the problem of placing Adena in some absolute chronological framework. He strongly states that ". . . on the basis of typology and stratigraphy, I seriously doubt that any Adena site in the Ohio Valley would have been in existence much after A.D. 1 or perhaps even earlier." (ibid. p. 289) While this statement may be a bit too definite, one could note that many of those dates after A.D. 1 were based on the carbon-black laboratory procedure and are therefore rather untrustworthy. With the exception of the Drake, Florence, and Cowan Creek Mounds, all the Adena dates seem to fall within the first 1500 years B.C., and recent evaluations of fluctuations in the upper atmospheric production of C^{14} make it likely that those radiocarbon dates around the time of the birth of Christ should be pushed back, perhaps as much as several hundred years. In New York, Ritchie (1969, p. 170-178, 181-201) places his Orient Phase at 1000-700 B.C. and the Meadowood Phase at 1000-500 B.C. The former phase has most of

the artifacts and burial customs common to Adena. The latter phase is distinguishable from Red Ocher sites in Michigan only by (1) the geographic location, (2) the fact that Meadowood burials contain more indications of widespread trade in luxury items, and (3) definite associations with Early Woodland ceramics. The Glacial Kame "culture" also appears to fall within this period of the first 1500 years B.C. and it is becoming increasingly clear that many of the "later" Old Copper manifestations do as well. (Halsey, 1966).

It may be of some interest to note that the area of western Lake Erie does not seem to show much evidence of occupation at this time. Survey work in southeastern Michigan by Brose and Fitting, and the surveys of northeastern Ohio by Earl J. Prah of the University of Toledo have revealed an apparent hiatus in the occupation of the old lake plain area from the end of the Middle Archaic period (ca. 1500 B.C.) until the transitional Middle-Late Woodland period (ca. A.D. 700). The significance of this negative evidence which is also duplicated in southwestern Ontario (John Lee, personal communication) will perhaps become apparent when some reasonable approximation of Early Woodland settlement systems is obtained.

At any rate, it seems clear that the Girdled Road site represents an occupation during this ill-defined and poorly understood period when Late Archaic and Early Woodland burial cults were flourishing throughout the eastern United States. The conclusions which can be drawn from the analyses of this site may perhaps dispel some of the confusion, at least in the limited area of northeastern Ohio.

CONCLUSIONS

While diagenetic soil conditions prevented the recovery of any significant sample of faunal remains, some inferences as to economic adaptation can be made from other data. The stratigraphic data, the topographic location of the Girdled Road site, and the lithic materials recovered all argue strongly for a limited-duration occupation. Although the midden itself was discontinuous, the maximum boundaries of occupation were about 20 feet by 15 feet. The rough ellipse appears to have enclosed an area of approximately 235 square feet. On the basis of modern ethnographic accounts pertaining to the Indians of the Upper Great Lakes, this would have been an area of floor space within a structure sufficient for

from three to eight individuals (cf. Brose, 1970b). Since no post-molds or features were encountered at the Girdled Road site, it would seem that no such structure was erected.

The total absence of ceramics also argues for a short-term occupation, probably by a group whose sexual composition was unbalanced with few (if any) females represented. The above data point rather clearly to the Girdled Road site as an example of a temporary hunting station occupied by a group of males. There was a surprisingly large number of unbroken artifacts recovered from approximately one-third of the total available site area. This probably indicates that the site was occupied several times for short periods. In this respect one might note that Dragoo (1963) has indicated that the variations in projectile point morphology reflected in the sample from Girdled Road may be chronologically significant.

The Girdled Road site thus represents an Early Woodland hunting station similar to other northern Ohio sites such as the lower levels at Mixter, and the Burrell Fort site (Shane, 1967). The analysis of lithic sources indicates that the occupants of the Girdled Road site either moved seasonally throughout the north-eastern third of the state of Ohio to obtain these materials, or were in contact with numerous localized groups located therein. While it is probable that exotic material such as Lake Superior copper was obtained by trade of some sort (Fitting and Brose [in press]) it is not likely that low-quality cherts and flints would have entered such a network. The implications are that the group experienced considerable seasonal mobility as a result of their economic adaptation. While this adaptation is imperfectly known, it must have included fairly large semipermanent or permanent villages such as Leimbach, as well as seasonal special-purpose extractive camps, presumably for hunting large mammals. There is no evidence for seasonal fishing or waterfowl-collecting camps, although too little site survey has been performed along the lake shore to evaluate this negative evidence. The evidence for horticultural or agricultural activity at this time level is not only extremely limited (Vickery, 1970) but is equivocal at best. The total settlement system of these populations thus remains rather ambiguous. Not until considerable further excavation has been done will we be able to discuss the inter-relationship of culture and ecology during the Early Woodland period.

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THE CLEVELAND MUSEUM OF NATURAL HISTORY

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MAY 3, 1971

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NOTES ON AN ADDITION TO THE FISH FAUNA OF THE MOWRY SHALE (CRETACEOUS) OF WYOMING

DAVID H. DUNKLE

ABSTRACT

The incomplete remains of the skull and skeleton of a diminutive ray-finned fish from the Mowry Shale (Middle Cretaceous) near Cody, Park County, Wyoming, is described as a previously unrecognized addition to the Mowry fish fauna. The basic organization of morphologic characters suggests tentative assignment of the specimen to the leptolepiform genus *Clupavus*.

INTRODUCTION

During the course of the 1970 American Western States Heritage Tour, co-sponsored annually by the Cleveland Museum of Natural History and the Martha Holden Jennings Foundation of Cleveland, a brief examination was made of exposures of the Middle Cretaceous Mowry Shale in the vicinity of Cody, Wyoming. On that occasion one of the youthful participants of the tour, Dale Shisler of Bartlesville, Oklahoma, recovered a partial but articulated skeleton of a diminutive fish. The Mowry Formation and equivalent strata of Wyoming and adjacent Rocky Mountain states have long been known for their myriads of disassociated scales and other occasional elements of fishes. The principal contributor to the description of some of these has been T. D. A. Cockerell (1919). In view of widely recognized difficulties in reasonably accurate interpretation of macerated skeletal parts, the presently described specimen is indicative of the continuing incompleteness of information about the Mowry fauna and emphasizes the importance of more complete, associated, but undescribed materials from the formation also available in various of the nation's museums.



The specimen (Cleveland Museum of Natural History 11045) was encountered in Mowry outcrops immediately west of State Route 120, 1.7 miles south of the Cody Airport in Park County. Various stratigraphic sections of the formation in the Cody area and their lithologies have been described by Reeside and Cobban (1960). Displayed are the head, in left lateral aspect, with an attached series of 27 vertebrae, recurved acutely and forwardly over the skull roof. Little actual osseous tissue is preserved. However, the sharp and distinct impressions in the highly siliceous, fine-grained matrix of, in part, both internal and external surfaces of neurocranial and visceral elements of the skeleton permits observation of a significant number of basic morphological characteristics. These are here interpreted as denoting definite leptolepiform affinity and, in fact, within this order of halecostome fishes tentative reference of the specimen to the genus *Clupavus* Arambourg (1950) is suggested. Because of ignorance of caudal fin structure and other pertinent details, specific diagnosis of the fish is considered unwarranted, at this time.

Deep appreciation is expressed to Dale Shisler for his donation of this interesting specimen to the Cleveland Museum of Natural History. The photograph and drawings have been provided by the Cleveland Museum staff members Bruce Frumker and Barbara Gardiner, respectively.

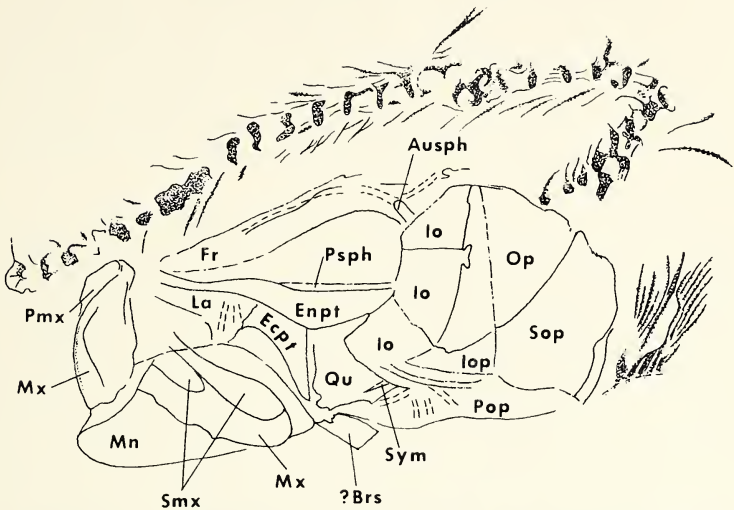
DESCRIPTION

The total preserved length of the specimen is 28.6 mm of which the head occupies 10.6 mm. The posterodorsal border of the skull roof is not preserved at the midline, but this transverse plane, as reconstructed, is presumed to mark the deepest dimension of the head, with a measurement little more than two-thirds of the head length. Neural spines and ribs are delicate and short. These features combine to indicate a very slenderly fusiform body habit.



Fig. 1. *Clupavus* sp. (CMNH 11045) from the Middle Cretaceous Mowry Shale near Cody, Park County, Wyoming. (A) Photograph and (B) habit sketch of the specimen, as preserved. Reproduction approx. $\times 6.6$. Explanation of abbreviations: Ausph, autosphenotic; ?Brs, branchiostegal; Ecpt, ectopterygoid; Enpt, entopterygoid; Fr, frontal; Io, infraorbital; Iop, interoperculum; La, lacrimal or preorbital; Mn, Mandible; Mx, Maxilla; Op, operculum; Pmx, premaxilla; Pop, preoperculum; Psph, parasphenoid; Qu, quadrate; Smx, supra-maxilla; Sop, suboperculum; Sym, symplectic.

B



In lateral aspect, the skull would appear to have only a slight dorsal convexity. Preorbital and postorbital lengths of the neurocranium are short. The relatively large, ovate orbit has an axial length one-third that of the head from snout to posterior margin of the opercular apparatus. The quadratomandibular articulation is situated below the midorbital length and the mandibular symphysis is prominent.

Of the bones of the skull roof, the impression of the smooth superior surface of the right frontal is to be observed almost in its entirety. Indicated are extremely long and attenuated elements. The bone bears the supraorbital sensory canal, which in the postorbital region branches into a mesial, parietal extension and a lateral connection with the infraorbital and main supratemporal canals. The lateral margin of the skull roof in the otic region is obscured by remnants of adhering bone. These, however, undoubtedly represent portions of the dermosphenotic, autosphenotic and pterotic bones. In this area there is rather wide separation and no conjunction of the dorsal extension of the preopercular sensory canal with the supraorbital and infraorbital canals. Dorsolaterally the posterior edge of the pterotic is adjoined by an axially short and somewhat transversely elongated extrascapular. Visible portions of the dorsal margin of the parasphenoid exposed above the medial edge of the entopterygoid traverse the orbit horizontally.

The bones surrounding the mouth, as preserved, are distended upwardly and forwardly. The oral length of the premaxilla is scarcely one-fifth that of the maxilla, which has a constricted proximal part and a ventrally convex expanded distal portion, surmounted with anterior and posterior supramaxillae. The dentition as revealed by the internal impression of a maxilla is reduced to a narrow oral band of minute, clustered teeth. The oral margin of the mandible rises rapidly from the robust symphysis to a high coronoid process.

The infraorbital series consists presumably of five elements. The impressions of radiating sensory-canal grooves suggest a moderately expanded lachrymal or preorbital bone as does the preserved evidence of the outline of the posteroventral second infraorbital. The third and fourth infraorbitals are much shorter and there are no traces of suborbital elements.

A characteristic triangular expanse of a quadrate shows below the second infraorbital. The anterior margin of this bone lies ver-

tically in a transverse plane. An oblique and anteroventrally directed articular facet for the symplectic suggests a vertical or only slightly forward inclination of the hyomandibula. The anteromesial and posteroventral limbs of the ectopterygoid meet in a nearly 90° angle. Although anterior autopalatine and posterior metapterygoid sutures are obscured, the entopterygoid would appear to be expanded.

The opercular apparatus is complete. Ventral horizontal and dorsal vertical rami of the preoperculum are of disparate length and height. The length of the horizontal limb is somewhat less than half the length of the skull. A mesial flange along the forward edge of the preoperculum is indicated and suggests intimate internal support of the element by the hyomandibula and quadrate as well as the shift of origin of adductor mandibulae muscles which was acquired by the advanced halecostomes (Gardiner, 1967). The operculum is the largest of the complex with an oblique ventral margin meeting the vertical anterior border in an acute anteroventral angle. The posterior edge of the operculum is continued downward and forward by that of the suboperculum in a broad sweeping arc. The interoperculum is horizontally elongated along with the ventral arm of the preoperculum which overlaps it widely. An impression of a bone beneath the anterior extremity of the preoperculum suggests that the branchiostegal rays were expanded and relatively few in number.

Of the 27 vertebrae preserved, the anterior 22 are considered abdominal and the remaining 5 caudal. The centra show little regional variation and are generally well ossified, with lengths slightly greater than their diameters. They are hourglass-shaped with very reduced notochordal perforations and bear laterally as many as three axial strengthening laminae. The proximal attachments of the neuropophyses with the centra are obscure but there appears to be a progressive gain in the robustness of these structures posteriorly. Epineural elements, as shown by delicate impressions across the neural spines, are definitely present in the midabdominal region. The proximal portions of the rib impressions recurve forwardly and lie parallel to the ventral borders of the vertebrae. Evidences of well defined parapophyses are absent.

From the point of low ventral attachment of the pectoral fin rays, the anteroventral limb of the cleithrum is short and constricted in comparison with the high and moderately expanded

dorsal ramus of the bone. The anterior margins of the two parts, meeting in a gentle forward concavity, are thickened into a mesially directed flange which forms the border of the opercular cleft. Little else of other girdle elements and of the radials can be ascertained. Pectoral fin rays number 7 in both the right and the left appendages, but may have totaled a few more. The rays of both fins are adpressed vertically along the posterior margin of the cleithrum. As impressed, the rays indicate long narrow fins, without evidence of axial jointing and with only the posterior rays dichotomizing.

DISCUSSION

The generic assignment of the presently described and incompletely revealed fish from the Mowry Shale may well be considered as extremely tenuous by many. It is tentatively offered, however, on the bases of general structures, proportions and relations of parts. Of fundamental significance in these connections are the attenuated frontals with the contained supraorbital sensory canals having parietal and infraorbital branches; absence of a confluence of the dorsal extension of the preopercular sensory canal with the supraorbital and infraorbital canals and consequent lack of a recessus lateralis (Greenwood and others, 1966) and similarities of mouthparts, the infraorbital elements, the hyopalatine complex and the opercular apparatus.

The genus *Clupavus* was defined by Arambourg (1950) for the reception of various small fishes from the Upper Jurassic of England and the Lower Cretaceous of Dalmatia, Jugoslavia and Gabon, which had originally been attributed to *Leptolepis*. Subsequently, *Clupavus* species have been recognized from the Cretaceous of Portugal (Ferreira, 1961); the Lower Cretaceous of the Congo (Casier, 1961); and the Upper Cretaceous (Cenomanian) of Morocco (Arambourg, 1954) and Lebanon (Patterson, 1967).

In the total brief literature concerning the genus there appears to be a general concurrence of opinion that *Clupavus* is a morphologic derivative of the halecostome fishes, through which narrow front the holostean-teleostean transition is thought most probably to have occurred. Within this framework *Clupavus* has been variously treated systematically: (1) together with the leptolepids within an advanced holostean level of organization (Greenwood

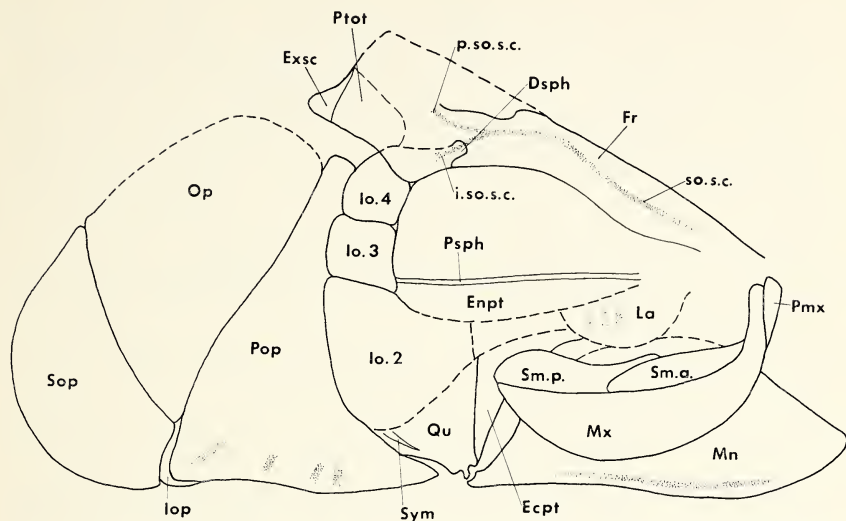


Fig. 2. Attempted reconstruction, in right lateral aspect, of the skull of the Mowry specimen (CMNH 11045) of *Clupavus*. Reproduction approx. $\times 10$. Explanation of abbreviations: Dsph, dermosphenotic; Ecpt, ectopterygoid; Enpt, entopterygoid; Exsc, extrascapular; Fr, frontal; Iop, interoperculum; Io 2, 3, and 4, second, third and fourth infraorbitals; La, lacrimal or preorbital; Mn, mandible; Mx, maxilla; Op, operculum; Pmx, premaxilla; Pop, preoperculum; Psph, parasphenoid; Ptot, pterotic; Qu, quadrate; Sm. a., anterior supramaxilla; Sm. p., posterior supramaxilla; Sop, suboperculum; Sym, symplectic; i.so.s.c., infraorbital branch of supraorbital sensory canal; p.so.s.c., parietal branch of supraorbital sensory canal; so.s.c., supraorbital sensory canal.

and others, 1966; Andrews and others, 1967); (2) at a teleostean level of organization from which the leptolepids are excluded as of lower level (Arambourg, 1954; Bertin and Arambourg, 1958); and (3) at a teleostean level of organization in which the leptolepids are included (Arambourg, 1950; Casier, 1961; Danil'chenko, 1964; Romer, 1966 and Patterson, 1967). The two most recent and comprehensive classifications of fishes (Greenwood and others, 1966; Andrews and others, 1967) favor the first of these three alternatives.

Romer (1966, p. 354) reports another North American occurrence of the genus *Clupavus*. No formal reference to such a prior assignment has been found. It is, however, thought possibly to pertain to *Leptolepis nevadensis* David (1941) from the freshwater Newark Canyon Formation of the Lower Cretaceous (Nolan, 1962), since Miss David compared that species most favorably to the same suite of diminutive species on which Arambourg erected *Clupavus*.

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KIRTLANDIA[®]

THE CLEVELAND MUSEUM OF NATURAL HISTORY

CLEVELAND, OHIO

OCTOBER 1, 1971

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DEVONIAN FISHES FROM CALIFORNIA

DAVID H. DUNKLE

Cleveland Museum of Natural History

and

N. GARY LANE

University of California, Los Angeles

ABSTRACT

The first occurrence of the well-known dinichthyid arthrodire *Dunkleosteus*, represented by disassociated and weathered bones, in the Quartz Spring Sandstone Member of the Lost Burro Formation (Late Devonian) in Inyo County, California, is reported. Of particular interest is the presence of teeth of cladodont and cochlodont sharks together with the *Dunkleosteus* bones.

This notice reports an original finding of weathered, disassociated remains of Devonian fishes from California. The specimens were collected by one of us (N. G. L.) north and 100 feet above the road passing through Lost Burro Gap (lat. $36^{\circ} 44' 59''$; long. $117^{\circ} 31' 19''$, northeast corner of the Ubehebe Peak 15' quadrangle, Inyo County, California). The specimens were obtained from thin-bedded cherty limestone and calcareous to dolomitic sandstone in the upper 20 feet of the Quartz Spring Sandstone Member of the Lost Burro Formation. This member constitutes the *Cyrtospirifer* Zone of MacAllister (1952) and a late Upper Devonian age has been indicated by studies of invertebrate fossils (Langenheim and Tischler, 1960), and conodonts (Youngquist and Heinrich, 1966). This age can now be corroborated on the basis of the presently noted vertebrate fossils.

The recognizable remains, deposited in the paleontological collections of the Cleveland Museum of Natural History, include two fragmentary elements of the dermal armor of a moderately large

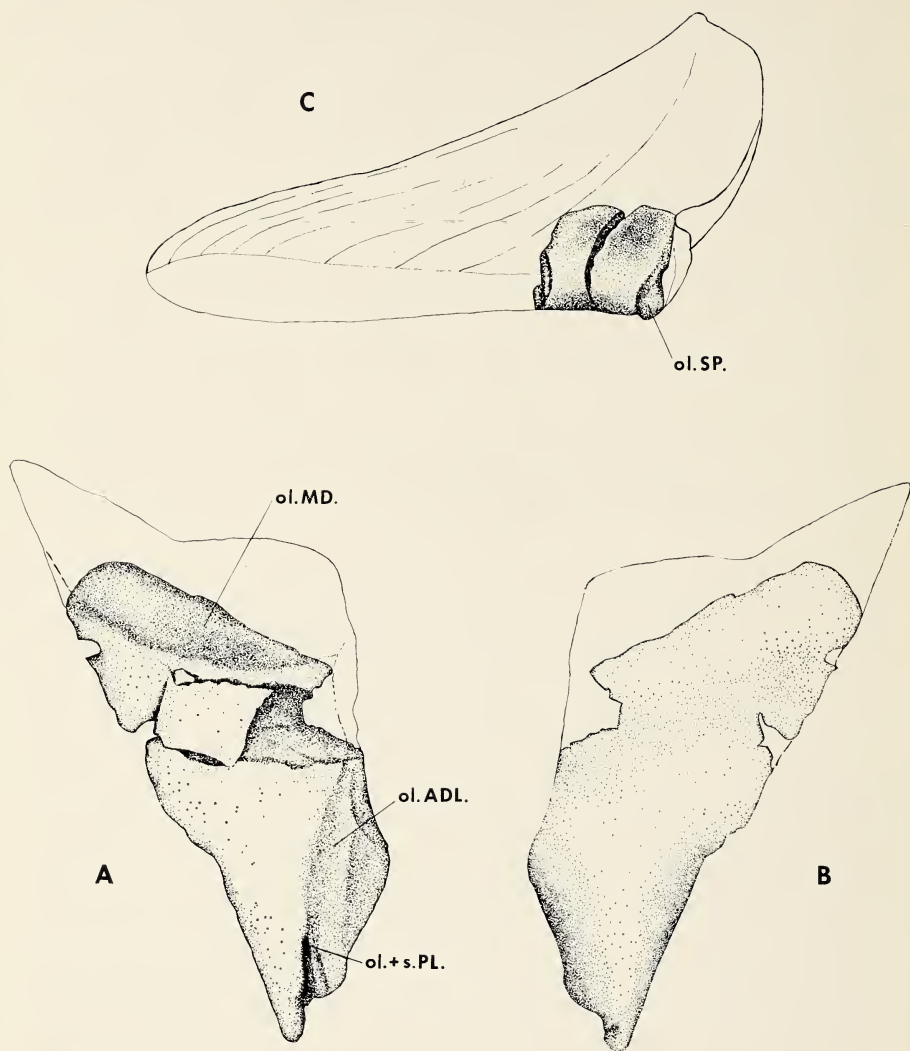


Fig. 1. Bones attributed to *Dunkleosteus terrelli* (Newberry) from the Quartz Spring Sandstone Member of the Lost Burro Formation (Late Devonian) in Inyo County, California. Sketches, as preserved, of right posterior dorsolateral plate (CMNH 8231) in (A) external and (B) internal views and left interolateral fragment (CMNH 8232) in (C) anterolateral aspect. Reproduction approx. $\times .45$ natural size. Abbreviations: ol. ADL, overlap area for anterior dorsolateral; ol. MD, overlap area for median dorsal; ol. SP, articular facet for spinale; ol. + PL, overlap area and sulcus for posterolateral.

placodermatous fish and the teeth of a shark and of a cochliodont. The placoderm bones are readily identifiable as the right posterior dorsolateral (CMNH 8231) and the left interolateral (CMNH 8232) plates of an arthrodire. In fact, comparative details of structure are so closely similar that the bones cannot be distinguished from the corresponding elements of the distinctive and well-known dinichthyid *Dunkleosteus*. The materials are illustrated (fig. 1) imposed on the outlines of appropriate bones of *Dunkleosteus terrelli* (Newberry) from the Ohio Shale. For present purposes further description is unnecessary.

The shark tooth (CMNH 8233), typically cladodont although generically indeterminate, is a relatively small example and consists of an expanded root having rounded extremities and a width almost equal to its length. The cross section of the principal cusp displayed is robust and although a little flattened or slightly concave on its labial side is without either lateral keels or vertical striation. A single pair of diminutive lateral accessory cusps is indicated. The recognized cochliodont nature of the other tooth (CMNH 8234) is based on the histologic structure of a basal layer of osteodentine and a superficial layer of tubular dentine whose parallel canals perforate the convex coronal surface perpendicularly.

Despite a lengthy awareness of the collective nature of the arthrodiran genus *Dinichthys* only a few of the indicated revisionary studies of the many species either originally or secondarily attributed to it have been made. Among those accomplished, however, Lehman's (1956) removal of three forms (*Dinichthys terrelli*, *D. intermedius* and *D. curtus*) (see also Eastman, 1907 and Dunkle and Bungart, 1940, 1946) from the Upper Devonian Ohio Shales to a new genus, *Dunkleosteus*, is of pertinent interest in the present connection. The combination of structural characteristics which distinguish *Dunkleosteus* from all other arthrodiran associates have been elaborated, especially by Heintz (1932), in detail. Of these and prompting this similar generic allocation, the new materials from California display the same overlap plus ingrown dentation of the sutural articulation between posterolateral and the posterior dorsolateral bones. Also, the interolateral presents the similarly shortened ventral lamina and the well-defined articulatory facet preserved laterally on the ascending lamina denoting the retention of a greatly reduced spinal element which among the presumably closely related dinichthyid assemblage is a unique feature of *Dunkleosteus*.

Dunkleosteus is best known for numerous remains and many individuals showing great variation in size in certain strata, notably the black Ohio Shale (Famennian) of Ohio and Kentucky, equivalent levels of the New Albany Shale in Indiana and north-central Kentucky and the Chattanooga Shale of Tennessee. Some fragments wholly reminiscent of the genus and possibly reworked into the basal Mississippian have been reported from Texas (Dunkle and Wilson, 1952). In addition, other species from the Upper Devonian of Morocco (Lehman, 1956) and of Europe (Obruchev, 1964) have been referred to *Dunkleosteus*. It is probable that future studies of other dinichthyid species (notably *D. magnificus*, Hussakof and Bryant, 1918, from the Rhinestreet Shale, *D. missouriensis* Branson, 1914, from the Grassy Creek Shale, among others) may prove to have the same generic affinity but at the present time no very great extension of the temporal distribution of *Dunkleosteus* can be projected.

The finding in California of these fishes, all representative of marine lineages, is not only of considerable paleogeographic importance but, in view of the meager available record of Devonian coeliodonts, is definitive of an interesting and, as yet rather uncommon, faunal association.

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THE CLEVELAND MUSEUM OF NATURAL HISTORY

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NUMBER 16

A CARBONIFEROUS LABYRINTHODONT AMPHIBIAN WITH COMPLETE DERMAL ARMOR

ALFRED SHERWOOD ROMER

Museum of Comparative Zoology, Harvard University

ABSTRACT

Specimens of a labyrinthodont, *Greererpeton burkemorani*, from the Lower Carboniferous of West Virginia, show an apparently complete body covering of dermal scales, indicating the impossibility of "skin-breathing" in this early amphibian.

It has been suggested by many workers interested in the history of vertebrate respiration that skin-breathing was a transitional stage in the shift from gill-breathing in fishes to lung-breathing in higher terrestrial vertebrates. This hypothesis, of course, arises from the fact that in modern amphibians the skin is naked and moist and much of the oxygen-carbon dioxide exchange takes place through the skin. I have, however, recently (Romer, 1972) pointed out that such an evolutionary succession is highly improbable. To begin with, it is generally agreed that lungs were already present in the rhipidistian crossopterygian fishes from which land vertebrates quite certainly derived — fishes completely ensheathed in an armor of thick bony scales. However, an important question remains — what was the condition of the body covering in the ancient amphibians of the Paleozoic, from which the modern orders were derived? It could be argued that lungs, even if present in the ancestral tetrapods, may have been too primitive and ineffectual in nature to carry the whole burden of respiration, and that a naked skin may have been early called upon as a breathing aid. To evaluate properly the worth of such a concept, it is necessary to resort to paleontology and attempt to determine the nature of the skin in older amphibian types.

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The living orders of amphibians — the Apoda (Gymnophiona), Urodela (Caudata), and Anura (Salientia) — are relatively modern groups. Almost nothing is known of fossils of the first group; urodeles go back only to the Cretaceous, last of the Mesozoic periods; frogs had developed by the mid-Mesozoic Jurassic Period, and one “pre-frog” (*Protobatrachus* or *Triadobatrachus*) is known from the Late Triassic. But amphibians originated far back, in Late Devonian times, and for the Late Paleozoic and even most of the Triassic Period — a stretch of time of close to one hundred and fifty million years — we find considerable faunas of amphibians, but amphibians quite distinct from the more modern types. Within these groups quite surely lay the ancestors of the later forms. What sort of body covering did these ancestors possess?

Two ancient groups have been advocated as possible ancestors — the Microsauria and the Labyrinthodontia. The microsaurians were small forms, usually but a few inches in length, whose remains are not infrequently preserved on slabs of shale which show not only the skeleton but also the nature of the skin. The skin is seen to have had a complete covering of bony scales; hence if the microsaurians were ancestors, the naked-skinned condition was surely a late acquisition.

However, current opinion (Parsons and Williams, 1963; Estes, 1965) favors the descent of the modern orders from the Labyrinthodontia, particularly the subgroup of this great order termed the Temnospondyli. The labyrinthodonts include a host of varied forms which were very prominent in Late Paleozoic and Triassic times. Some labyrinthodonts were small, but many ranged up to the size of a modern alligator or crocodile. For these forms, determination of the nature of the body covering is in general a matter of difficulty. Seldom are their remains discovered in flattened slab form, as are those of the little microsaurians. Usually they are found as three-dimensional burials in clays and shales. After death and before burial, the soft parts tended, of course, to rot, and skin as well as muscles and viscera were generally separated from the skeleton of the cadaver; further, excavation of the skeleton and its preparation in the laboratory has tended to do away with any remnants of the body covering of the living animal.

Almost invariably the ventral portion of the original fish-scale covering is retained in labyrinthodonts as a series of gastralia (or abdominal "ribs"), very useful in protecting the bellies of these low-slung animals (fig. 1). As regards the rest of the

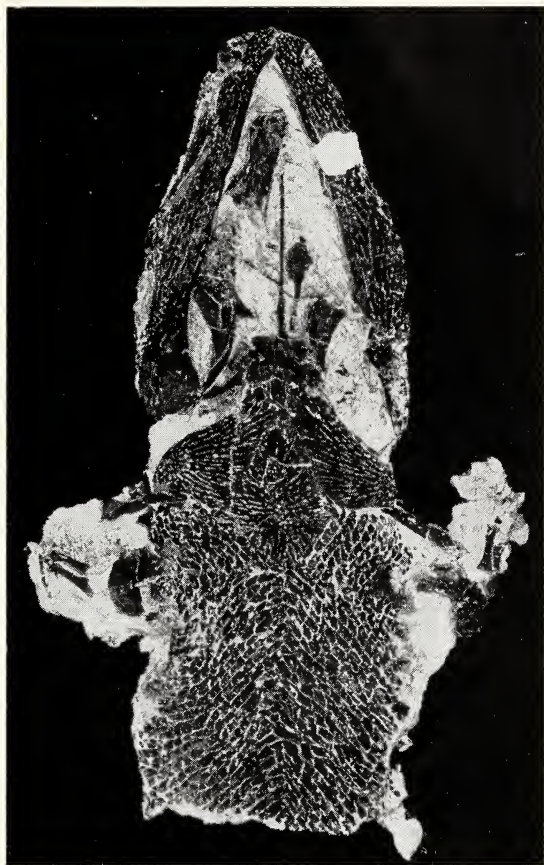


Fig. 1. Ventral view of head and part of trunk of a specimen of *Greererpeton*, CMNH 11090, showing the lower surface of the jaws, dermal shoulder elements and most of the ventral abdominal shield of gastralia. About 1/3 natural size.

body covering, knowledge is, as expected, meagre. As I noted in my recent paper (1972), dorsal squamation has been known in only four labyrinthodonts: *Eryops*, *Trimerorhachis*, *Archegosaurus*, and *Actinodon*. All four are temnospondylous labyrintho-

donts — the generic group from which the modern orders are very probably descended — but all four are, unfortunately, of relatively late (Permian) age. It would be of considerable interest to acquire data as to the nature of the body covering in the older members of the group.

As we descend the geologic scale, however, labyrinthodont remains become relatively rare. Numerous specimens have been found in the Upper Carboniferous — the Pennsylvanian Period of American nomenclature — but for the most part they represent forerunners of the Permian groups. From the entire Lower Carboniferous (Mississippian), there had been recovered, until recently, only a single rather poorly preserved labyrinthodont skeleton (*Pholidogaster*, Romer, 1964); a considerable amount of material of the oldest amphibians, the ichthyostegids, of the Late Devonian, has been collected but for the most part remains unstudied. We thus had very little knowledge of the structure of the older labyrinthodonts, and no adequate data upon which to judge the presence or absence of bony squamation in the most ancient members of the group.

This picture is now considerably altered by recent discoveries in the Mississippian of West Virginia. Most rocks of that age are marine in nature, but at Greer, near Morgantown, West Virginia, there occurs high up in the wall of a limestone quarry, a layer containing continental sediments (Hotton, 1970, p. 1-5). This layer is the Bickett Shale, a basal member of the Mauch Chunk Group, representing the upper portion of the Mississippian deposits of the area. In this shale there have been found for many years fragmentary remains of amphibians, and in the last few years the Cleveland Museum of Natural History has undertaken, under the direction of Dr. David H. Dunkle and with the assistance of William Hlavin and others, excavation of the bone layer there. Most of the bones are in a single layer exposed in the nearly vertical face of the quarry. Despite the difficulties of the task, the Cleveland Museum has already excavated to a variable depth (as much as 14 feet in one area) the main bone-bearing layer for some 50 feet along the quarry face. This layer proves to contain a nearly solid mass of amphibian remains, skulls and complete skeletons, closely packed and flattened dorso-ventrally so as to include, in essentially slab form, all the "hard"

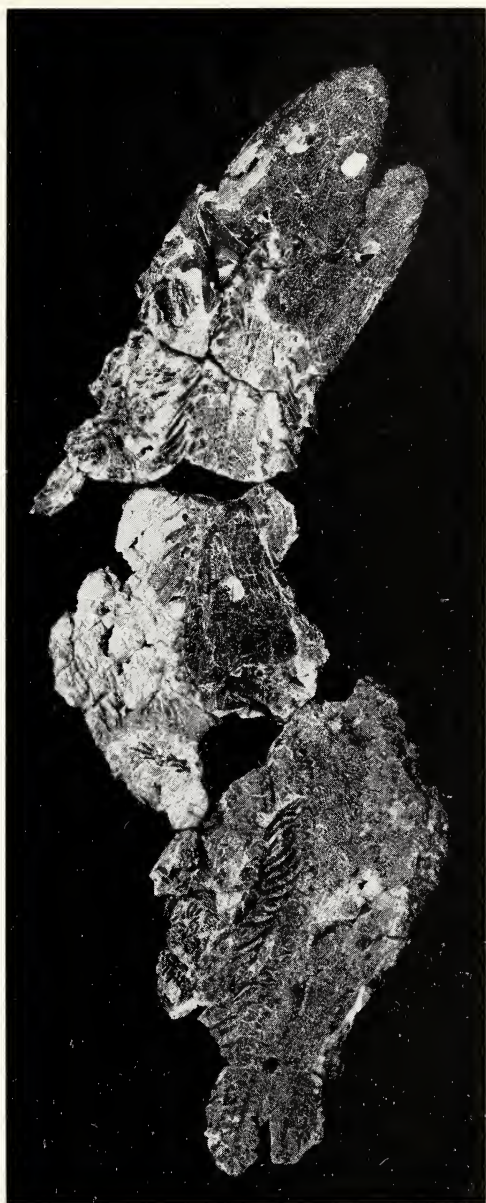


Fig. 2. Dorsal view of a slab containing much of the skeletons of three individuals of *Greererpeton* CMNH 11036, 11034 and 11082. Quantities of dorsal scales are visible, particularly posteriorly. About 1/6 natural size.

remains of the animal — not merely the skeleton, but also the skin if, in the process of burial, it had not been completely disintegrated and floated away from the main portion of the cadaver.

The most common amphibian in the bed is *Greererpeton*, a form of which I gave a preliminary description in 1969. The exact systematic position of this genus is at present none too certain. It is, however, a temnospondyl in vertebral structure and hence, in at least a broad sense, a member of the general group of labyrinthodonts from which modern orders are not improbably descended, although *Greererpeton* is certainly not in the direct ancestral line. In this genus the stout series of gastralia is to be found (fig. 1) covering the belly region. But in addition many of the specimens of this form show over the dorsal region a highly developed series of scales, subcircular in form and averaging 1.0 to 1.5 mm in diameter (figs. 2-4). The skin in which they were embedded in life had quite surely become more or less disintegrated before burial, and hence we cannot be sure of the exact nature of the scale pattern in life. It is, however, evident that even *post mortem* the disintegrating skin often retained a definite pattern of the arrangement of the scales in regular rows. There had rather certainly been a reduction in scale size from the situation seen in typical crossopterygians (cf. for example, Romer, 1966, fig. 100), and a lessening of the deep overlapping of scales seen in these ancestral forms; however, in some cases (cf. fig. 4) there are indications that a certain degree of overlapping persisted in the members of scale rows.

Rather surely the general body squamation in *Greererpeton* was not as complete as in crossopterygians, and some gaps may have existed between scales. But certainly the scale covering was such as to exclude the possibility of any great degree of skin breathing. It is, of course, not impossible to argue that some labyrinthodonts may have developed a naked skin. But the discovery of a well-developed scale covering in one of the oldest labyrinthodonts known, as well as evidence of a similar skin structure in a number of later temnospondyls, adds weight to the theory very generally accepted by paleontologists, that a scaled body sheathing was present in the ancestors of the modern



Fig. 3. Posterior portion of the block shown in figure 2, mainly skull and skeleton of CMNH 11082. Dorsal scales, preserved in more or less of a regular pattern, as seen along most of the region to the right of the vertebral column. Disarticulated gastralia are seen along the left margin. About 1/3 natural size.

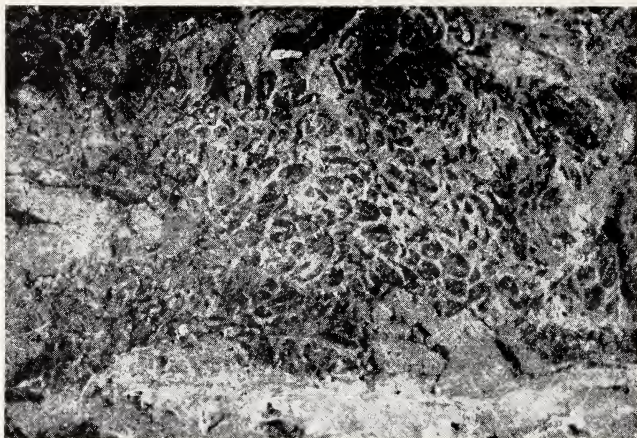


Fig. 4. A small portion of the dorsal region of a skeleton, CMNH 11070, about natural size, to show arrangement and possible overlapping of scales.

amphibians and that the development of a naked skin came about at a relatively late period in amphibian evolution.

Credit is due Virginia Heisey of the Cleveland Museum of Natural History for skillful preparation of the *Greererpeton* specimens, and to Bruce Frumker, of the same institution, for the excellent photographs from which plates 1-3 were derived.

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NOTES ON THE MORPHOLOGY OF *ACANTHERPESTES* (MYRIAPODA, ARCHYPOLYPODA) WITH THE DESCRIPTION OF A NEW SPECIES FROM THE PENNSYLVANIAN OF WEST VIRGINIA

J. J. BURKE

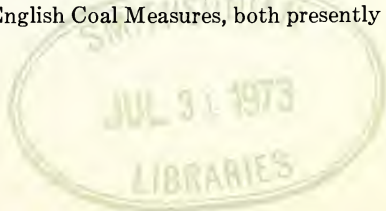
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ABSTRACT

Study of a large fossil myriapod from the Pennsylvanian Allegheny Group in Monongalia County, West Virginia, necessitated comparison with specimens representing various species of the Upper Carboniferous euphoberiid genus *Acantherpestes*, including *Acantherpestes major*, type species of the genus. This investigation determined that, contrary to previous interpretations, *Acantherpestes* was a "flat-backed" myriapod, characterized as follows: Tergites moderately arched transversely, with two rows of spines on each side of the metazonite, one row comprising simple reduced subdorsal spines flanking the dorsal midline, the second row consisting of long, stout, lateral spines arising near the lateral border, subhorizontally or horizontally disposed, and bifurcate, with basal spinelets. Lateral spines, prolonged beyond the body of tergite, sheltered the laterally extended, elongate feet. Sternites entire, prosterna and metasterna not divided medially, with "cups" housing exsertile sacs situated close to median line, and spiracles adjoining the coxal region laterally. Coxal regions with sternal inflations, terminating in outward-facing coxal sockets. Feet composed of five podomeres, the second quite elongate.

Scudder's interpretation of *Acantherpestes* as an amphibious myriapod is disputed; the feet are regarded as having been adapted for weight bearing and efficient locomotion, rather than to serve as swimming appendages; exsertile sacs are considered to have absorbed water to combat dessication, rather than having a gill-like function for underwater respiration.

American species of *Acantherpestes* include *Acantherpestes major* Meek and Worthen, *Acantherpestes inequalis* Scudder, and *Acantherpestes clarkorum* sp. nov. Also herewith assigned to *Acantherpestes* is the American species *Euphoberia hystricosa* Scudder, and the familiar English Coal Measures myriapod *Euphoberia ferox* (Salter). In addition, at least one American species, and another from the English Coal Measures, both presently unnamed, are attributable to *Acantherpestes*.



Myriapod taxa from the Upper Carboniferous of Czechoslovakia, attributed by Fritsch to *Acantherpestes* and *Euphoberia*, differ greatly from species comprising the latter genera, having: (1) tergites more arcuate in transverse section; (2) flank spines more upright; (3) subdorsal spines much longer and stouter; (4) sternites not entire—prosterna and metasterna divided medially; and (5) sternal structures widely at variance with those of *Acantherpestes* and *Euphoberia*. It is evident that new genera should be established for the reception of these Fritsch species.

The myriapod from the Pennsylvanian of West Virginia, described as a new species, *Acantherpestes clarkorum*, is distinguished mainly by its large size, subdorsal spines reduced to nodes, small tubercle near outer termination of lateral furrow, and long lateral spines, bifurcate at midlength, having the anterior prong about one-third the length of the posterior, and prominent basal spinelets exceeding the anterior prong in length.

INTRODUCTION

The present article stems from the discovery of a large fossil myriapod in the Pennsylvanian Allegheny Group in Monongalia County, West Virginia (Barlow, 1969). Study of this specimen showed it to be a representative of the genus *Acantherpestes* Meek and Worthen, and a new species, but prior to this determination it was necessary to make extensive investigation of various fossil myriapods from the Upper Carboniferous of North America and Europe. Completion of this work, in consequence, has been delayed.

The paper is divided into two parts. The first embodies brief notes on the morphology of *Acantherpestes*, sufficient, it is hoped, to furnish basic information on the structure of the genus as we now know it. The second part combines provenance and other details of the West Virginia specimen, followed by systematic paleontology, including an emended diagnosis of *Acantherpestes*, plus a diagnosis and description of the new species, accompanied by pertinent discussions. A compilation of references cited throughout the article follows the second part.

ACKNOWLEDGMENTS

Several persons and institutions, both here and abroad, have contributed in one way or another to assist this project, and to all of them I extend hearty thanks. Specimens have been loaned for study by Dr. Bernard Kummel and Miss Vickie Kohler of the Harvard Museum of Comparative Zoology; Dr. H. W. Ball and Dr. S. F. Morris of the British Museum (Natural History); Dr. Porter Kier of the National Museum of Natural History; Dr. John Carter of the University of Illinois; Dr. Eugene S. Richardson of the Field Museum; Mr. Stephen LeMay of Chicago, Illinois; and Mr. Walter Dabasinskas of Monticello, Wisconsin. I am indebted to Dr. Alec Panchen of the University of Newcastle-upon-Tyne for information concerning fossil myriapod localities in the English Coal Measures. Dr. John Hower of Case Western Reserve University conducted an X-ray analysis of the specimen. I am grateful to the Thomas Clark family of Morgan-

town, West Virginia, for the opportunity to study this fossil, which they have since donated to The Cleveland Museum of Natural History.

Initial preparation of the specimen was by Mr. Peter Hoover of Case Western Reserve University. His help is fully appreciated, along with that of three staff members of The Cleveland Museum of Natural History: Miss Virginia Heisey, for additional preparation; Mr. Brant Gebhart, for illustrations; and Mr. Bruce Frumker, for photography.

TERMINOLOGY

An explanation of some of the terminology employed in this article is pertinent at this point. A body segment (or diplosomite) of *Acantherpestes* is composed of a single dorsal plate, the tergite, which overlies two ventral plates, the sternites, each of which bears a single pair of legs. Two divisions of the tergite are recognized. The anterior of these, the prozonite, is smooth, and is overlapped by a portion of the tergite anterior to it. The posterior division of the tergite, the metazonite, is elevated above the prozonite and overlaps the prozonite of the tergite posterior to it. The metazonite of *Acantherpestes* bears spines and other distinctive features which are of use in making specific determination within the genus. Figure 1 is a diagrammatic sketch of a single tergite of *Acantherpestes*, with significant details labeled.

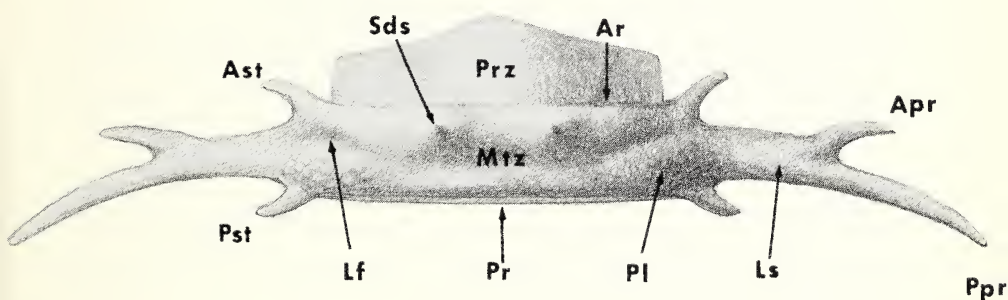


Fig. 1. Diagrammatic dorsal view of a tergite of *Acantherpestes*, with salient details of morphology indicated. Abbreviations: Apr, anterior prong of lateral spine; Ar, anterior ridge; Ast, anterior spinelet; Lf, lateral furrow; Ls, lateral spine; Mtz, metazonite; Pl, posterior lobe; Ppr, posterior prong of lateral spine; Pr, posterior ridge; Prz, prozonite; Pst, posterior spinelet; Sds, subdorsal spine.

Most of the designations used in figure 1 have been employed by previous writers in dealing with these myriapods, or are self-explanatory. Two new terms are introduced. A depression which arises posterior to the subdorsal spine and extends toward the anterolateral corner of the metazonite is called the *lateral furrow*. From the standpoint of orientation of these fossils, which may be damaged or fragmentary, the lateral furrow

is the most important topological feature of the body of the tergite. In damaged specimens, where the preservation is such that the prozonite-metazonite relations of successive tergites are obscure, those furrows, extending obliquely outward and forward on opposite sides of the metazonite, are a means of differentiating between the anterior and the posterior regions of the body. In addition, in fragmentary specimens, if the subdorsal spine and its accompanying lateral furrow are preserved, it is possible to determine whether the right or the left side of the metazonite is represented.

The term *posterior lobe* is applied to a swollen area of the metazonite which borders the lateral furrow posteriorly and merges laterally with the lateral spine. This swollen area varies in prominence in different species of *Acantherpestes*, and is usually characterized by gridlike ornament.

ABBREVIATIONS

The following abbreviations of institution names are employed in this article: BM, British Museum (Natural History); ISM, Illinois State Museum; MCZ, Harvard Museum of Comparative Zoology; UI, University of Illinois; USNM, National Museum of Natural History.

I

NOTES ON THE MORPHOLOGY OF *ACANTHERPESTES*

STRUCTURE OF *ACANTHERPESTES* AS INTERPRETED BY MEEK AND WORTHEN (1868) AND SCUDDER (1882, 1890)

Up to the present, all described material from North America which appears assignable to the genus *Acantherpestes* has been derived from the siderite nodules of the Middle Pennsylvanian Francis Creek Shale of the Carbondale Formation (the so-called Mazon Creek beds of Grundy County, Illinois).

Meek and Worthen (1868a) in the course of describing Mazon Creek specimens, established the myriapod genus *Euphoberia*, basing the genus on a small species, *Euphoberia armigera*. A second species, *Euphoberia major*, was distinguished from *armigera* on the basis of its larger size.

At that time, however, Meek and Worthen appear to have had at hand at least two large specimens, one of which they compared with Salter's (1863) *Eurypterus?* (*Arthropleura*) *ferox*, stating that they had little doubt that it was congeneric with that species.

Later (1868b) Meek and Worthen gave a fuller description of the larger species under the name *Euphoberia?? major*. Much of the description is a repetition of the original, but there are some additional observations on

features which the writers regarded as distinguishing *Euphoberia?? major* from *Euphoberia armigera*. A figure, evidently intended to illustrate the differences between the species, accompanied the description of *Euphoberia?? major*. Because the description and the figure gave rise to a misunderstanding of the species which has persisted to the present, I am reproducing the full text and figure below.

EUPHOBERIA?? MAJOR, M. AND W.

Euphoberia major M. and W., 1868. Am. Jour. Sci., vol. XLV, p. 26.

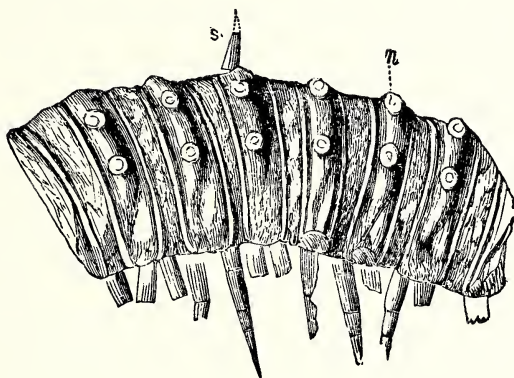


Fig. 2. (From Meek and Worthen, 1868b, p. 558) Cut illustrating *Euphoberia?? major* M & W = *Acantherpestes major* M & W.*

This name was proposed by us for a much larger fossil than the typical species of the genus, though we unfortunately yet know it only from mere fragments, one of the best of which is represented by the annexed cut. If as long in proportion as the other species, it probably attained a length of 12 to 15 inches, and must have presented a formidable

* Original caption: "*Euphoberia?? major* / Cut of a fragment consisting of six of the dorsal scutes, and parts of two others, with one of the dorsal spines (s) broken and lying in the matrix. The nodes (n) are evidently spine bases. Some of the legs are seen below."

appearance. The node-like prominences, marked *n* in the figure, are evidently the bases of spines that have been broken away. One of these, however, is seen lying in the matrix at the point marked *s*. Another specimen (not figured) shows a direct view of the dorsal side, compressed flat. In this, traces of two rows of these node-like prominences are seen along the middle, while a row of spines can be seen projecting out into the matrix on each side.

This latter specimen so nearly resembles a fossil figured by Mr. Salter in the Quarterly Journal of the Geological Society of London, vol. XIX, p. 84, fig. 8, from the Staffordshire Coal Measures under the name *Eurypterus?* (*Arthropleura*) *ferox*, that we can scarcely entertain a doubt that they are congeneric. Indeed, if it were not for the fact that the species *ferox* has its spines each provided with three, instead of two, prongs, we would even suspect that our specimen might possibly belong to the same species. Mr. Salter thought his specimen probably a part of the central lobe of a trilobate *Eurypterus*, or some allied genus, an opinion he would not have entertained for a moment (provided we are right in our suggestion respecting its relations to our fossil) if he had seen a specimen showing a side view of even a few of the segments, with their legs attached. At any rate, our fossil is certainly distinct from the genus *Arthropleura* of Jordan and von Meyer, which is almost beyond doubt a crustacean.

This larger type, for which we have proposed the specific name *major*, not only differs in size from the typical species *armigera*, but also presents the marked difference of having its dorsal scutes much shorter and deeper, in proportion to their size. Indeed, as we are not positively sure that it has two segments below for each one of the dorsal scutes, we are by no means clearly satisfied that it belongs to the same genus as *armigera*, or that it may not even be even much more widely removed from that type. It is therefore only provisionally that we have placed it in this genus. This appearance, however, may possibly be in part due to the oblique manner in which the specimen has been compressed in the matrix.

If other specimens should be found, showing it not to agree with the typical species of the genus *Euphoberia*, in having two segments below for each one above, it will of course have to be removed from that genus, in which case it might be called *Acantherpestes*.

It is my feeling that Meek and Worthen were concerned about other features of the morphology of *Euphoberia*?? *major* in addition to the number of sternites per tergite. I have no doubt that the unfigured specimen, with the two rows of nodes running along the middle and a row of spines projecting out into the matrix on either side, represented what we now know as *Acantherpestes*. However, this specimen appears to have been lost, and the description is so general that it might apply to almost any species of the genus. Evidently the resemblance to Salter's *Eurypterus?* (*Arthropleura*) *ferox* was much closer than Meek and Worthen thought—Salter's drawing shows three large prongs, but there are really only two prongs, and he greatly exaggerated the size of the anterior spinelet, which is not at all prominent.

I suspect that Meek and Worthen did not figure this specimen showing

the two rows of lateral spines, nor declare it the type of their species, because they were under the impression that *Euphoberia?? major* possessed three rows of spines on each flank, and probably assumed that in the unfigured specimen a third set was present, concealed in the matrix beneath those that were projecting out on each side. Note that they felt sure that Salter would not have confused his specimen with *Eurypterus* or a similar form “. . . if he had seen a specimen showing a side view of even a few segments with their legs attached.” Probably Meek and Worthen had only one specimen preserved (as they thought) in this fashion, and it is the subject of the drawing accompanying the description (reproduced in my figure 2). It is apparent that Meek and Worthen regarded this figure as showing the specimen in lateral view. It is only when it is interpreted in this light that their statement (1868b, p. 559) that in addition to differing from the species *armigera* in size, the species *Euphoberia?? major* “. . . presents the marked difference of having its dorsal scutes much shorter and deeper in proportion to their size” becomes intelligible. This constitutes an adequate effort to diagnose the differences between *Euphoberia?? major* and *Euphoberia armigera*, and I take the view that this figured specimen is the type of *Euphoberia?? major*.

Woodward (1872) presented a drawing copied from that of Meek and Worthen (1868b) along with most of the text of their description. He alluded to *Euphoberia?? major* as *Euphoberia? major*, but applied the generic name without question to the Salter species *ferox*, which he had examined, using the combination *Euphoberia ferox* (Salter). However, there is a curious omission in Woodward's quotation of the Meek and Worthen text—he does not include the portion dealing with the characteristics which they felt distinguished *Euphoberia?? major* from *Euphoberia armigera*. Neither does he allude to Meek and Worthen's hypothetical genus *Acantherpestes*.

Scudder (1882), although he was convinced that the tergites of *Euphoberia?? major* each bore two sternites, after expressing his displeasure at the use of hypothetical names, nevertheless accepted the generic name *Acantherpestes* and employed the combination *Acantherpestes major* Meek and Worthen. He reproduced (1882, text fig. 5) the Meek and Worthen illustration, at the same time enlarging upon their interpretation of the species.

In effect, Scudder saw the Meek and Worthen figure as showing, in lateral view, several segments of a deep-flanked myriapod which had a cylindrical body and essentially circular cross-section. In Scudder's con-

cept, the animal bore three rows of spines (represented in the figure by spine bases) on each flank. The lower row of spine bases he took to represent lateral spines, the second row he called "pleurodorsals," and the row at the top of the figure, subdorsals. This viewpoint of the structure of *Acantherpestes* was illustrated by Scudder in 1882 (text figs. 3, 4, and pl. 10).

MORPHOLOGY OF THE GENUS BASED ON RESTUDY OF
THE TYPE OF *ACANTHERPESTES MAJOR* MEEK AND WORTHEN

The specimen figured by Meek and Worthen as *Euphoberia?? major*, which I take to be the type of that species, and consequently the type of *Acantherpestes major* Meek and Worthen as well, is repositied in the paleontological collection of the Department of Geology, University of Illinois. Dr. John Carter, as curator of that collection, kindly loaned me the specimen for study. The type bears the number UI X-504; formerly it was part of the Illinois State Museum collection under the number ISM 11120. The fossil was lightly coated with magnesium oxide and

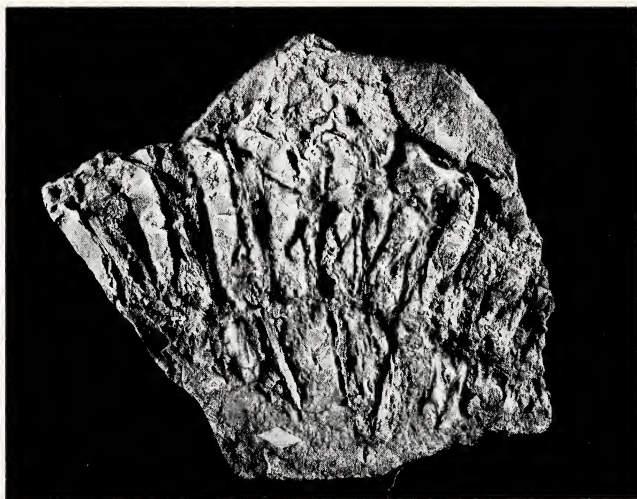


Fig. 3. *Acantherpestes major* Meek and Worthen. Type, UI X-504, from the Francis Creek Shale, Carbondale Formation, Pennsylvanian, at Mazon Creek, Grundy County, Illinois. Anterior portion of specimen facing left. Slightly oblique dorsal view, X 1.

photographed (figs. 3, 4). In figure 4, various morphological features of the specimen are labeled, using the terminology illustrated in figure 1.

Figures 3 and 4 indicate that the Meek and Worthen illustration, as represented in my figure 2, is inaccurate in many respects, but principally in failing to show details in the upper left portion (the anterior part of the right side of the animal). Here, in addition to the spine bases depicted by Meek and Worthen, my photograph shows at least five distinct lateral furrows on the right side, demonstrating beyond any doubt that the spine bases associated with these furrows are the bases of the right subdorsal spines of the animal. It is obvious that the dorsal midline passes between this row of spines and the left subdorsals, which Scudder mistakenly identified as "pleurodorsals." Scudder correctly identified the lower row of spine bases as laterals. On the opposite (right) side, the row of lateral spines is not preserved; the specimen is not complete in this region. Some portions of spines remain (one of which is shown in figure 2). However, Meek and Worthen seem to have overlooked a damaged lateral spine, which is displaced and lies on the right lateral flank of the posterior half of the fossil. The spine is widely bifurcate, and the prongs appear to deviate from the plane of the main shaft.

It is evident from the above that in UI X-504 the median line passes

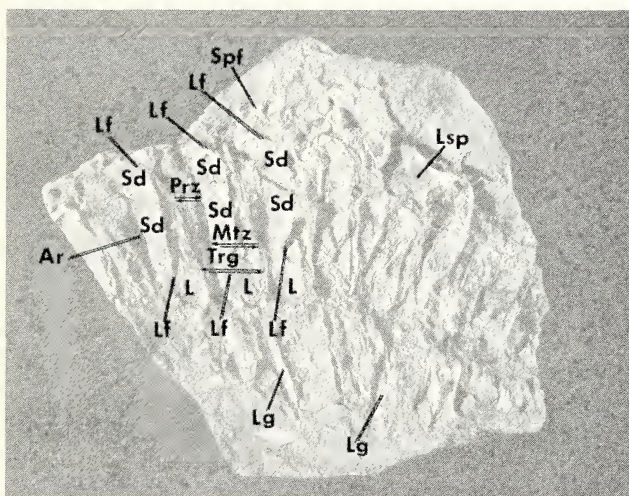


Fig. 4. *Acantherpestes major* Meek and Worthen. Type, UI X-504, same as fig. 3, but pertinent morphological features labeled. Abbreviations: Ar, anterior ridge; L, lateral spine base; Lf, lateral furrow; Lg, leg; Lsp, lateral spine; Mtz, metazonite; Prz, prozonite; Sd, subdorsal spine base; Spf, spine fragment; Trg, tergite.

between the two rows of subdorsal spines, and there were only two sets of spines—the massive laterals and the less prominent subdorsals. The

tergites of UI X-504 are only moderately arched from side to side, and for the most part the specimen is showing in dorsal, rather than lateral, view. It follows that *Acantherpestes*, as indicated by the type species, was not, as Scudder thought, a deep-flanked myriapod, circular in cross-section, with three rows of spines on each side. On the contrary, it was a "flat-backed" myriapod, in the sense meant by Gill (1924). Two specimens in the Harvard Collection, MCZ 7437/1a/1b and 7437/2, seem properly assigned to *Acantherpestes major*. Both consist mainly of sternal segments that are gently convex ventrally, which would indicate that this species is nearly elliptical in cross-section.

An investigation of the material described as *Acantherpestes major* by Scudder in 1882 indicates that he was dealing with at least two species of the genus, neither of which bears close resemblance to UI X-504. Examination of his specimens shows that in no case did they conform with his concept of *Acantherpestes* as a long-flanked myriapod with a cylindrical body having three rows of spines on each flank. I have not seen his specimens described and figured in 1890 as *Acantherpestes inequalis* and *Euphoberia hystricosa*, but their affinities are evidently with *Acantherpestes* as exemplified by the type species. The species *hystricosa* is quite definitely an *Acantherpestes*, and it is here designated *Acantherpestes hystricosus* (Scudder) n. comb.

All of the American specimens and species cited above accord in the features characteristic of *Acantherpestes* in keeping with my interpretation of the genus, and, when sufficiently complete, show tergites having moderate curvature from side to side, the metazonites of which display near each lateral border a single row of massive lateral spines, and on each side of the dorsal midline, a row of shorter subdorsal spines.

ACANTHERPESTES IN THE ENGLISH COAL MEASURES

These same features hold also for representatives of the genus in the English Coal Measures, where *Acantherpestes* is represented by at least two species. Through the kindness of the authorities of the British Museum (Natural History), I have been able to borrow a cast (BM I. 1063) of the specimen described by Salter (1863) as *Eurypterus?* (*Acanthropleura*) *ferox*, and find it assignable to *Acantherpestes*, rather than to *Euphoberia*, as suggested by Meek and Worthen (1868a, 1868b) and Woodward (1872). (Actually, as I have noted previously, Meek and Worthen were probably comparing Salter's species with a specimen of *Acantherpestes*, but I have not been able to find this specimen, which may be lost, and the description could apply to almost any species of *Acantherpestes*.) In any case, I am here-

with designating the English species *Acantherpestes ferox* (Salter) n. comb.

In addition, I believe that the specimens described by Gill (1924) and Brade-Birks (1928) which are derived from the Middle Coal Measures Crow Coal at Crawcrook, near Ryton-on-Tyne are referable to *Acantherpestes* as well. However, this small form, with distinctive lateral spines, quite evidently represents a species other than *ferox*, to which it was attributed, but apparently with some hesitation, by Gill and Brade-Birks.

The short papers by these English authors contributed much to clarifying the characteristics of the taxon which I regard as constituting *Acantherpestes*. Gill (1924) stated: "Some of the fossil millipedes at present known as species of *Euphoberia* do appear to have been more or less cylindrical, but it may be suggested that that is a reason for separating them generically from *ferox* rather than for assuming that *ferox* also was cylindrical." This observation followed his noting that the specimen he was describing appeared to be a "flat-backed millipede," and his contrasting the curvature of its tergites and attitudes of the lateral spines with those represented in Woodward's (1887, pl. 1, fig. 11) restoration. As a matter of fact, the tergites and the lateral spines of most of the specimens figured in Woodward's plate 1 do not appear to accord with the strongly arched tergites and distinctly inclined lateral spines shown in the restoration. Furthermore, the British Museum cast of Salter's type of *Acantherpestes ferox*, which I have at hand, does not indicate marked curvature of the tergites and shows that the lateral spines were sub-horizontally disposed. Although Woodward (1887, p. 8) noted that he did not feel that "these large Myriapods" were as round as indicated by Scudder, it is apparent that he was much influenced by Scudder in preparing his restoration.

Brade-Birks (1928) gave further demonstration that the tergites of the Crawcrook species were not strongly arched and that the spines were nearly horizontal in disposition. He also showed the structures of the sternites properly oriented; both Scudder (1882) and Woodward (1887) confused anterior with posterior in specimens exhibiting the sternites, and oriented these structures accordingly. However, I gather from Brade-Birks' description that he viewed the structures extending from the midline to the spiracles as coxae, fused at the midline and penetrated closely adjacent to the midline by the so-called branchial cups. Brade-Birks' "walled pits" lateral to the "cups" he considered bases of telepodite joints. Examination of USNM 33039, the specimen illustrated by Scudder (1882, pl. 11, figs. 1-4) would indicate otherwise. Scudder thought that the portion illustrated in fig. 2 represented casts of portions of sternites; actually these are fossilized exoskeletal structures seen in ventral view. Each plate appears to be a fairly typical sternite, penetrated close to, and on each side of the midline, by the "branchial cups." Between the "cups" and the spiracles, the sternites are produced ventrally as dilatations that terminate in obovate outward-facing coxal sockets. These appear to be characteristic coxal sockets which in the American species of *Acantherpestes* receive the relatively short but stout coxae, which in turn are joined to the very long first telepodite joints. Woodward (1887) found two joints preceding the long joint, but I suggest that restudy of his specimen will determine that only one, the coxa, precedes the elongate podomere, as in modern Symphyla.

It is of interest to note that in the illustrations of all three authors, Scudder, Wood-

ward, and Brade-Birks (who pointed it out in his specimen), the midlines of the sternites deviate from those of the tergites, suggesting that after death the ventral and dorsal segments of these animals slipped askew, tearing the sternites away from the tergites to which they were probably joined by arthrodial membrane. I find no support for Woodward's (1887) inference that there was an "overhang" of the tergites beyond the sternites. In one of the Harvard specimens, MCZ 7437/2, identified as *Acantherpestes major*, some of the sternites and tergites are showing in such close proximity as to leave little doubt that they were joined at their lateral extremities.

The species of *Acantherpestes* from the English Coal Measures do not attain the size, nor display the specialized spines of some of the American forms, but this is in keeping with their being possibly exclusively of Westphalian B age, whereas the American representatives of the genus are from younger (Westphalian C and D) beds.

II

ACANTHERPESTES CLARKORUM SP. NOV. FROM THE ALLEGHENY GROUP, PENNSYLVANIAN, OF WEST VIRGINIA

HISTORY OF THE SPECIMEN

The fossil myriapod described in the following pages was discovered by Alan, Bruce, and Quentin Clark, the young sons of Mr. and Mrs. Thomas Clark of Morgantown, West Virginia. It was found in the spoil bank of an abandoned coal strip mine about 10 miles (16.9 km) south of Morgantown. The specimen for the most part was contained in two pieces of siltstone (since cemented together) with only the very tips of some of the subdorsal spines penetrating an overlying piece of rock. Numerous fossil leaves, mainly *Neuropteris*, were associated with the myriapod specimen, which was covered with a very adherent matrix. The rock, however, was transversed by cracks, and had been subjected to weathering: beneath the matrix, the surface of the fossil consisted in many places of powdery iron oxide.

The original skeleton of this myriapod was impregnated with calcium carbonate, but diffraction X-ray analysis of the fossil, conducted by Dr. John ^{Howes} Brower of the Department of Geology, Case Western Reserve University, determined that the skeleton now consists of siderite with a small percentage of chamosite.

Preparation was by means of an air abrasive unit. Although this resulted in loss of the powdery oxide surface, I do not think that any other method of preparation would have served much better. Despite some evident damage otherwise, the ornament of the posterior lobes of

several metazonites is still showing—an indication that the effects of preparation were not altogether too drastic.

A small exploratory opening on the underside of the stone containing the fossil showed no trace of sternites nor legs. No further preparation was attempted in this region because of the possibility of serious damage to the specimen.

PROVENANCE

The abandoned strip mine in which the specimen was found lies about 0.8 mile (1.3 km) south of the village of Browns Chapel, in Clinton District, Monongalia County, West Virginia, on the south side of the Gladesville-Halleck road, 0.5 mile (0.8 km) east of the intersection of that road and U. S. Route 119.

The coal that was strip mined at this site was previously identified by the West Virginia Geological Survey (Hennen and Reger, 1913) as the Lower Kittanning. However, Mr. Robert S. Reppert and Dr. James A. Barlow, present members of the survey, on the basis of recent field studies, informed me (letter, Feb. 2, 1973) that the 1913 designation was in error, and that the coal is actually the Lower Freeport. At the time of the 1913 report, a misidentification of the Brush Creek Coal of the Conemaugh Group as the Upper Freeport Coal of the Allegheny Group gave rise to the assumption that the coal at the site where the myriapod fossil was found was separated from the presumed Upper Freeport by an interval of nearly 200 feet (61 m), and consequently represented the Lower Kittanning Coal of the Allegheny Group.

The Upper Freeport Coal is sparsely shown or missing in the area where the fossil was found, but Reppert and Barlow state that its place is indicated by the base of the Thornton flint clay, which they have traced throughout the region. The coal of the strip mine lies about 70 feet (21.3 m) below the base of the Thornton flint clay in that vicinity, an interval that indicates that the coal in question, which is 4.5 feet (1.4 m) thick at this place, represents the Lower Freeport Coal of the Allegheny Group. The pieces of siltstone containing the fossil were not found in place, but came from the spoil bank of the mine. However, the rock is doubtless derived from the ferruginous siltstones associated with the coal, and very likely came from a 35-foot (10.7-meter) siltstone unit immediately overlying it.

SYSTEMATIC PALEONTOLOGY

Class ARCHIPOLYPODA Scudder, 1882

Family EUPHOBERIIDAE Scudder, 1882

Genus *Acantherpestes* Meek and Worthen, 1868, emended

Diagnosis: Medium size to very large Upper Carboniferous myriapods. Prozonites and metazonites fused to form single tergite. Tergites laterally expanded; moderately arched. Prozonites smooth, overlapped by metazonites. Metazonites elevated, with no more than a single row of large lateral spines along each flank, and on each side of the dorsal midline a single row of shorter subdorsal spines. Lateral spines long, massive, subhorizontally to horizontally directed, evenly or unevenly bifurcate, bearing two main prongs, and with spinelets at base. Subdorsal spines simple; spikelike, curved laterad, or reduced to nodes. Metasternites and prosternites undivided medially, with spiracles lateral to coxal sockets and openings for exsertile sacs near midline medial to coxal sockets. Sternites with dilatations in coxal regions terminating in outward-facing coxal sockets. Feet with five podomeres, and second podomere very elongate.

Type species: *Acantherpestes major* Meek and Worthen, 1868.

Referred species: *Acantherpestes ferox* (Salter) n. comb.; *Acantherpestes inequalis* Scudder; *Acantherpestes hystricosus* (Scudder) n. comb.; and *Acantherpestes clarkorum* sp. nov.

Distribution: Upper Carboniferous; Westphalian B and ?C, England; Westphalian C and D, U.S.A.

Some anatomical features not included in my diagnosis which may embody details limited only to a species rather than characterizing the genus as a whole, are also known. Woodward (1887) described portions of three heads, apparently attributable to *Acantherpestes ferox*. The mouth parts are not preserved. The head exceeds the body segments (exclusive of spines) in width. The front half is somewhat inflated and the posterior half bears four tumid lobes. The two lateral and smaller of these lobes comprise the ocellaria, which bear numerous ocelli. An antennal socket is found anterior to the ocellarium at the anterolateral angle of the inner lobe. A deep median groove which separates the inner lobes probably represents the epicranial suture. In the same paper Woodward describes a telson that probably pertains to *Acantherpestes* also. Possibly two segments are represented and only the posterior portion represents the telson proper. It bears four spines directed posteriorly; the two nearest the median line are longer and more robust. The anterior portion may comprise the metazonite of the penultimate segment; the spines appear to be normal lateral spines which are directed posteriorly because of breakage.

Nothing definite can be said of the segments immediately posterior to the head. However, Scudder's (1890, pl. 33, fig. 2) figure of *Acantherpestes inequalis*, although plainly poorly executed, is of much interest. The head is shown as somewhat wider than the body segments exclusive of spines. The first four segments are represented as shorter than those posterior to them, and the lateral spines progressively decrease in width from the fifth to the first.

Euphoberia, as exemplified by the type species *Euphoberia armigera* Meek and Worthen, bears closer resemblance to *Acantherpestes* than any other Carboniferous myriapod. However, although specimens of *Euphoberia* may show the same sets of spines (lateral and subdorsal) as *Acantherpestes*, the lateral spine in *Euphoberia* never attains the extravagant development that characterizes it in *Acantherpestes*. Along with the short lateral spine, the sternites of *Euphoberia* which, as in *Acantherpestes*, are not divided medially, do not show dilatations, and the openings of the coxal sockets do not face outward; in consequence the coxae were directly ventrally, rather than laterally or dorsolaterally. Spiracles were present, situated essentially as in *Acantherpestes*, but if there were also openings for exsertile sacs I have not been able to detect them in the few specimens that I have at hand. As a rule, species of *Acantherpestes* greatly exceed those of *Euphoberia* in size, but the small *Acantherpestes* from the English Coal Measures described by Gill (1924) and Brade-Birks (1928) does not appear to have been much larger than some examples of *Euphoberia*.

The genus *Sandtheria* Fritsch, 1899, shows some interesting euphoberiid resemblances. The dorsal midline is flanked on each side by a row of simple subdorsal spines. However, laterally, on each side, instead of the large lateral spine of *Acantherpestes*, the metazonites of *Sandtheria* bear a single small node, smaller than the subdorsal spines. The ventral side of *Sandtheria* is unknown. Apparently the spines and their arrangement in *Chonionotus* Jordan, 1856, are similar to those of *Sandtheria*, and in the absence of the characteristic lateral spine of *Acantherpestes*, the Jordan genus bears no real resemblance to the latter, despite the implications of Meek and Worthen (1868a) and Scudder (1882, 1885) revived more recently by Hoffman (1969). *Chonionotus*, contrary to Hoffman, has not been reported from North America; the type species, *Chonionotus lithanthraca* is derived from beds of Westphalian age near Saarbrücken, West Germany.

Species presently comprising the genus *Paleosoma* Jackson et al, 1919, from the English Coal Measures, were originally attributed to *Acantherpestes* and *Euphoberia* by Baldwin (1911). *Paleosoma* is clearly distinct from either of the latter genera, being extremely "flat-backed" and having lateral extensions of the tergites in the form of keels, very short prozonites, no subdorsal spines, and two distinct pleurites per tergite.

Ironically enough, the myriapods from Nyran which Fritsch (1899) attributed to *Acantherpestes* come close to Scudder's "long-flanked" concept of *Acantherpestes*, and consequently differ in that respect from *Acantherpestes* proper. The subdorsal spines of the Czechoslovakian species are long, robust and bifurcate, contrasting with the reduced, simple or nodelike subdorsal spines of *Acantherpestes*, and their "lateral" spines are directed dorsolaterally, rather than subhorizontally or horizontally, as in *Acantherpestes*. As regards the sternites, neither Fritsch nor Verhoff (1926) appear to have taken into account the fact that in *Acantherpestes*, as Scudder's figures (1882, pl. 11, figs. 1-4) indicate, the metasterna and prosterna are not divided, as they are in Nyran forms. Of the three structures displayed in Verhoff's "coxosternopleurites" the outermost certainly has the appearance of a spiracle and the inner represents a coxal socket. The third

feature, which occurs between the two just cited, but nearer the coxal socket, although approximating in position the coxal sac opening in certain modern millipedes, is much larger and more complex than that of any millipedes of which I know, and may mark the location of an organ with a function other than those of respiration or water absorption. Certainly in position it does not correspond to the "cups" which are situated medial to the coxal sockets of *Acantherpestes*, in essentially the same situation as the structures in Symphyla that contain exsertile sacs.

It is obvious that these species which Fritsch attributed to *Acantherpestes* clearly represent another and yet to be established genus. Also, a new genus is called for to include the Nyran taxa which Fritsch grouped under *Euphoberia*. These differ from both *Acantherpestes* and *Euphoberia* in the rounding and depth of their flanks, in type and disposition of spines, in showing medial separation of the sternites, and in having short prosterna devoid of spiracles, along with long metasterna which carry sternal spines.

***Acantherpestes clarkorum** sp. nov.**

Figs. 5, 6

Diagnosis: A large species, approaching *Acantherpestes major* in size. Anterior ridge occupies less than half the length of metazonite, and bears two subdorsal spines, here reduced to nodes. Small tubercle at or near outer termination of lateral furrow. Lateral spines large, length of each nearly equal to width of body of metazonite, and bifurcate at midlength. Posterior prong longest, bowed gently posterolaterally. Anterior prong about one-third length of posterior, extends anterolaterally in gentle arc recurving toward tip. Basal spinelets large, exceeding anterior prong in length, the anterior recurved, the posterior nearly straight.

Holotype: CMNH 3917, a string of 25 diplosomites or portions of diplosomites preserved in dorsal view.

Occurrence: Siltstone overlying Lower Freeport Coal (Westphalian D), Allegheny Group, Pennsylvanian Series, Upper Carboniferous.

Locality: Coal strip mine about 0.8 mile (1.3 km) south of the village of Browns Chapel, Clinton District, Monongalia County, West Virginia, on the south side of the Gladesville-Halleck road, 0.5 mile (0.8 km) east of the intersection of that road and U.S. Route 119 (Lat. 39° 29' 15'' N, Long. 79° 54' 45'' W) United States Geological Survey 7.5' Gladesville, West Virginia quadrangle.

* The species name is in recognition of Bruce, Alan, and Quentin Clark, who found the specimen upon which the species is based.

Description: The specimen exhibits, in dorsal view, and in various stages of preservation, 25 tergites disposed in a sinuous curve, and measures somewhat more than 25 cm over the curvature. There is no definite indication of either head or telson, although an indeterminate remnant beyond and to the right of the anterior end may represent a part of the head. In general the segments of the posterior portion show better preservation. All of the tergites have undergone compression to some extent, and some show longitudinal cracks as well. Counting from the anterior end, to and including tergite 13 there is noticeable flattening of these elements, and the surfaces of the segments are obscure, although the lateral spines of the right side are well shown. However, all of the lateral spines, which were once rounded in cross-section, are now flattened and almost paper thin in places. In comparison with segments of *Acantherpestes* which have not been distorted, tergites 14 to 20 appear to have suffered least damage and compression. The last three tergites are much flattened, having split along the midline and spread apart; the posteriormost is incomplete.

The surfaces of the metazonites are elevated above those of the prozonites, and each metazonite along its anterior border is fused with a prozonite. The prozonites are smooth and in life, probably to a considerable extent, each was overlapped by the metazonite of the tergite anterior to it. Here, however, some of the prozonites show greater exposure than normal and some are entirely exposed, possibly because after death, the decomposing body of the animal was torn by water currents prior to burial. The prozonites are less than the metazonites in length, and show their greatest length along the midline where the anterior border comes to an apex.

The anterior ridge is not especially prominent and tends to diminish sharply in height laterally. As a rule, it occupies less than half the length of the metazonite. On each side of the midline it bears a single subdorsal spine, here reduced to a node. Most of these nodes are broken away at the top, but the right subdorsal spines of the third tergite from the posterior end of this specimen is complete. A few others are essentially complete, and broken portions extracted from an overlying slab of rock into which the spines extended confirm that they were low nodes, rather than spikelike spines. The subdorsals are round to somewhat attenuate transversely, and their anterior slopes are continuous with the anterior slopes of the metazonites.

The lateral furrows are shallow where they originate posterior to the subdorsal spines, but expand and deepen in their anterolateral course. Anteriorly they are walled by the posterolateral slopes of the anterior ridges. A small lateral tubercle is usually found at the termination of the lateral furrow near the base of the anterior spinelet of the lateral spine.

Bounding the lateral furrows posteriorly are the moderately developed posterior lobes. Each is narrow and least swollen where it originates posterior to the subdorsal spines, becoming inflated and gradually expanding anteriorly before merging with the lateral spine. Most of the posterior lobes of this specimen have suffered extensive damage. Nevertheless, several of them preserve the gridlike ornament which seems generally to characterize these regions of the metazonites of *Acantherpestes*.

The midportion of the metazonite posterior to the anterior ridge is flattened or gently concave and meets with a moderate posterior ridge which extends transversely, but not beyond the posterior lobes. In general these ridges are poorly preserved in CMNH 3917.

The lateral spines arise from the sides of the metazonites. If the tergites of this fossil retained their original curvature and could be viewed in cross-section, the lateral borders

of the metazonites would be seen to extend beyond the spine bases. In view of the state of preservation of this specimen, no reliable measurements of the width of metazonites in relation to length of lateral spines can be obtained. It appears to me that the spine length may have been nearly equal to the width of the metazonite, but this is only a rough estimate.

These spines extend directly outward from the sides of the metazonites before bifurcating at midlength, although they expand slightly before branching into two prongs. The posterior prong is the longer and indicates the greatest length of the spine. It prolongs the posterior border of the main shaft without interruption, although from the place of bifurcation it bows gently posterolaterally. The anterior prong is about one-third the length of the posterior, extends anterolaterally in a gentle arc, and is actually slightly recurved near the tip.

The basal spinelets are relatively quite large. The anterior spinelet arises nearest to the base of the spine proper. It is nearly two-fifths longer than the anterior prong of the latter, and shows the same tendency to recurve. The anterior spinelet overlaps the posterior spinelet of the spine preceding it. The posterior spinelets are about a millimeter shorter than the anterior spinelets, but show slight curvature.

It is difficult to obtain meaningful measurements of a compressed specimen such as this, consequently the following figures (in mm) are, at best, only approximate: Length, tergite, 9.5; length, metazonite, 5.7; width, metazonite, 20.0 (estimated); length, lateral spine, 20.0 (estimated); length, posterior prong, 9.6; length, anterior prong, 2.9; length, anterior spinelet, 4.9; length, posterior spinelet, 4.0.

Discussion: The holotype of *Acantherpestes clarkorum* appears well differentiated from certain previously described specimens which have been attributed to *Acantherpestes*, although the specific relationships of some of the latter remain to be clarified. The strong anterior ridges and the type of subdorsal spines (as indicated by spine bases) exhibited by the metazonites of *Acantherpestes major* do not characterize the metazonites of *Acantherpestes clarkorum*, and the single lateral spine associated with the type of *Acantherpestes major* is entirely different from those of my West Virginia species. The superb specimen in the collection of the National Museum of Natural History, USNM 33038, described by Scudder (1882, p. 151-154, pl. 11, figs. 6, 8, 11) as *Acantherpestes major* is clearly distinguishable from *Acantherpestes clarkorum* if only on the basis of its nearly evenly bifurcate lateral spines and its characteristic laterally curving subdorsals.

Scudder also (1882, p. 154, 155, pl. 11, figs. 1-4) included under *Acantherpestes major* another specimen, USNM 33039, which on examination proves to represent a species entirely distinct from the latter, and also from the presumably yet to be established species to which USNM 33038 should be attributed. Scudder did not orient USNM 33039 correctly; in his figure 1 (op. cit.) the four articulated tergites showing in dorsal view are posteriorly disposed in relation to the rest of the segments. The lateral spines, which Scudder called "pleurodorsals" are inaccurately represented. Two of them are sufficiently preserved to show that they closely resembled those of *Acantherpestes clark-*

Fig. 5. *Acantherpestes clarkorum* sp. nov. Holotype, C.M.N.H. 3917, from siltstones overlying the Lower Freeport Coal, Allegheny Group, Pennsylvanian, near Browns Chapel, Clinton District, Monongalia County, West Virginia. Dorsal view, X 1.



orum. The subdorsals flank the midline and are reduced to nodes, as in my species, and the resemblance extends even further, for in USNM 33039 small lateral tubercles also mark the outer terminations of the lateral furrows. The tilted anteriormost metazonite of USNM 33039 appears to have undergone little damage and its gentle curvature from side to side indicates that the tergites were not strongly arched in cross-section. Unfortunately, only small portions of the prozonites are preserved, and the compressed lateral spines are difficult to trace with certainty, but I think this specimen may prove to be conspecific with *Acantherpestes clarkorum*.

Scudder (1890, p. 424-426, pl. 33, figs. 1, 4) described three additional specimens, all of which, despite the poor quality of his figures, seem assignable to *Acantherpestes*. I have not been able to study this material at first hand, because I do not know where it is repositied, if indeed it is still preserved. Under the name of *Acantherpestes inequalis*, Scudder included two specimens. The first of these (op. cit. p. 424, 425, pl. 33, fig. 2) shows several fragmentary lateral spines, and one nearly complete, which closely resemble those of *Acantherpestes clarkorum*. Other details of the figure are too vague for comparison, however. The second specimen (idem. p. 426, pl. 33, fig. 4) does not seem at all related to the first, but the spines illustrated suggest to some extent lateral spines of the type which I attribute to *Acantherpestes major*.

As noted above, Scudder (1890, p. 426, pl. 33, figs. 1, 3) described a third specimen at that time. To this he gave the name of *Euphoberia hystricosa*, but I have no doubt that the species should properly be referred to *Acantherpestes*. Scudder was mistaken in his orientation of the animal. The lateral furrows indicate that his "shorter anterior portion" is the anterior portion of the metazonite, and the "longer and blunter" prong of the lateral spine is the posterior, as is generally the case in *Acantherpestes*. The long, robust anterior ridge and a lateral spine described as having prongs "... only slightly divergent and subequal ..." with basal spinelets "... apparently clearly separated ..." from the spine shaft clearly distinguish this species from *Acantherpestes clarkorum*.

Scudder was in error in stating that this tendency for the basal spinelets not to merge with the shaft of the lateral spine, and the presence of an anterior ridge on the metazonite, does not characterize *Acantherpestes ferox* (Salter). True, Salter's (1863, fig. 8) original illustration does not clearly indicate an anterior ridge per se, and it is quite misleading in showing the anterior basal spinelets as greatly exaggerated in size and forming integral parts of the lateral spines. However, the British Museum cast of Salter's type shows relatively small anterior spinelets, rather distinct from the main shaft, and small but definite anterior ridges. It is also evident from the figures of Woodward (1887), Gill (1924), and Brade-Birks (1928) that the somewhat disparate basal spinelets are characteristic of English Coal Measures representatives of *Acantherpestes*. In this, as well as in their smaller size, they differ from *Acantherpestes clarkorum*; *Acantherpestes ferox* differs also in having spikelike subdorsal spines, and the form from Crawcrook described by Gill and Brade-Birks is distinguished from my species by the exceptionally long posterior prongs of the lateral spines.

The environmental relationships of *Acantherpestes* have given rise to considerable discussion. Scudder (1882) originated the concept that these were amphibious myriapods, basing his conclusions on the structure of the feet, which he regarded as adapted for swimming, and the presence on the sternites of so-called branchial cups, which he interpreted as housing gill-like organs used for respiring under water. However, the elongate foot of *Acantherpestes*, with podomeres described by Scudder (1882, p. 146)

as "... not cylindrical but compressed and slightly expanded, strengthened also on the flattened surface by longitudinal ridges ..." seems to me to be better interpreted as a powerful and efficient walking limb, resembling in structure the walking legs of some terrestrial insects, notably beetles, in being adapted both for bearing the weight of those heavy arthropods and for efficient locomotion on land.

As for the "branchial cups," they probably housed exsertile sacs of the type found in Symphyla, and occupy the same position as the exsertile sac openings in the latter. In *Hansiella agilis*, Teigs (1947) has demonstrated that these sacs are used for the absorption of water. Similar structures are found in Paupoda, in primitive insects, and are

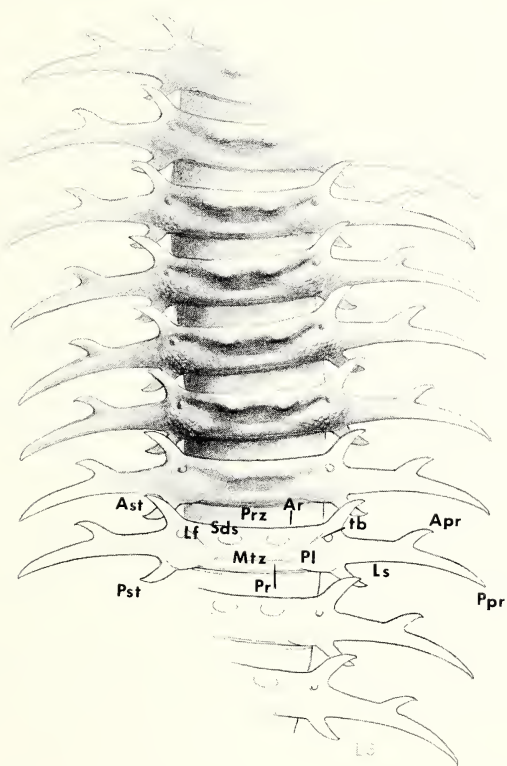


Fig. 6. *Acantherpestes clarkorum* sp. nov. Restoration of tergites (not corrected for compression). Dorsal view, X 1. Abbreviations: Apr, anterior prong of lateral spine; Ar, anterior ridge; Ast, anterior spinelet; Lf, lateral furrow; Ls, lateral spine; Mtz, metazonite; Pl, posterior lobe; Ppr, posterior prong of lateral spine; Pr, posterior ridge; Prz, prozonite; Pst, posterior spinelet; Sds, subdorsal spine; Tb, tubercle.

represented by coxal sacs in some modern millipedes. In the Myriapoda, one of their functions seems to be that of absorbing water as a means of combating dessication, and their presence in *Acantherpestes* does not demonstrate that representatives of that genus were in consequence amphibious.

What appears to have been the evolutionary sequence leading up to *Acantherpestes* also supports the conclusion that these were terrestrial animals. The stock from which this line was derived were probably small myriapods, possibly near *Euphoberia* in size, or even smaller. They must have been long-flanked, with cylindrical bodies, which bore upright or nearly upright spines; the legs were probably relatively short and not particularly stout. Evolution evidently proceeded in the direction of increase in size and development of legs suited to bear the increased weight, along with elongation of these appendages, to provide speedier locomotion. With increased size and faster gait, predators became less of a problem, and there was less need for spines purely as a means of protection. The long flanks were lost, the subdorsal spines became reduced, and the body expanded laterally—probably initially to provide shelter for the lengthening legs.

What followed appears to have been one of the most fascinating developments in the history of the Myriapoda. As the body expanded laterally to produce the "flat back" characteristic of *Acantherpestes*, the lateral spines came to be directed essentially horizontally, providing further protection for the lengthening legs, thus functioning in the same way as the paranota or keels of modern millipedes. It is also likely that in species such as *Acantherpestes clarkorum*, in which the subdorsal spines were much reduced, the broad tergites and extended lateral spines were employed to separate masses of matted leaves as the animal forced its way into them in search of food. The lifting and penetrating power in this case could have been supplied, as noted by Manton (1954, 1961) in modern millipedes, by drawing in the legs and pushing upward and forward with them. In this connection it might be noted that the anterior lateral spines of *Acantherpestes inequalis*, progressively decreasing in width cephalad, formed, together with the head, a wedge that would have facilitated penetration of leaf litter by the animal.

Figure 7 represents an attempt at restoration of a diplosomite of *Acantherpestes* as seen in posterior view, illustrating in cross-section the relationship of the essentially horizontal lateral spines to the elongate legs.

Protected from most predators by sheer size, *Acantherpestes* was probably able to move about freely. These myriapods may have ventured into open areas of the lowlands bordering the Carboniferous swamps, and were probably able to withstand some exposure to direct sunlight, as Causey noted for *Brachycybe* (Manton, 1961). Having retained the water-absorbing exsertile sacs, it seems reasonable that, as Manton suggests for *Brachycybe* and related millipedes, *Acantherpestes* may even have obtained water from drops of dew. By this device the Carboniferous form could have staved off dessication under dry conditions.

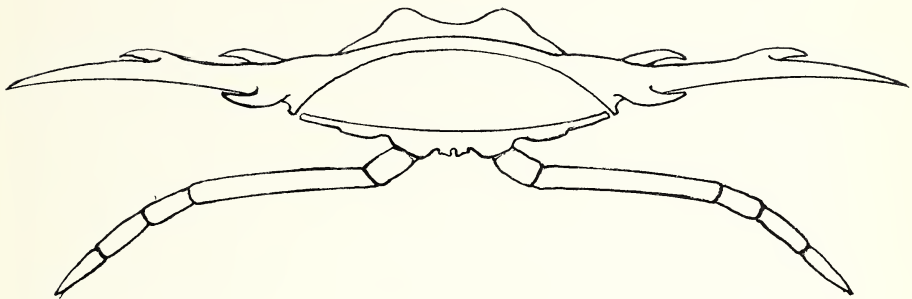


Fig. 7. Diagrammatic posterior view of a body segment of *Acantherpestes* (author's interpretation).

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ADDITIONS TO THE 'CRINOID FAUNA OF THE AMES LIMESTONE, BROOKE COUNTY, WEST VIRGINIA

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ABSTRACT

Descriptions of inadunate crinoids from the Ames Limestone, Conemaugh Group, Upper Pennsylvanian, of Brooke County, West Virginia, and Guernsey County, Ohio, pertain to the following taxa: (1) *Delocrinus segedii* sp. nov. related to *Delocrinus brownvillensis* Strimple, but differing in lesser height of dorsal cup, deeper basal impression, higher extent of basals on cup walls, and smaller primanal; (2) *Appalachiacrinus erwini* gen. et sp. nov., a laudonocrinid, differing from other laudonocrinids in greater height of dorsal cup, resembling *Laudonocrinus* in flatness of infrabasals, slight upflaring of infrabasal circlet, greater width and lesser curvature of C radial, and somewhat similar axillary primibrachs, but also resembling species of *Anchicrinus* and *Athlocrinus* in convexity of basal, radial and anal plates and presence of pits at angles of plates; and (3) *Parethelocrinus occultater* sp. nov., characterized by a globose dorsal cup, with shallow and wide basal concavity, convex downflaring infrabasals, radials having prominent flat forefacets, tertanal concealed by C primibrach but partly within cup, quartanal resting on secundanal; cup ornament finely granulose.

INTRODUCTION

As indicated in a previous study (Burke, 1973), several species of Pennsylvanian crinoids from the Ames Limestone, Conemaugh Group, of Brooke County, West Virginia, are known only from the Upper Pennsylvanian of the Appalachian region. Subsequent study has determined three additional species from the Brooke County Ames, hitherto undescribed and likewise unknown beyond the confines of the Appalachian basin. These taxa, mainly represented by specimens in the collection of the Cleveland Museum of Natural History (CMNH) but in one instance also by material loaned by the Carnegie Museum (CM), are described in the following pages.

I wish to express my appreciation to Dr. John Carter and the Carnegie Museum for the loan of specimens. I am also grateful to the West Virginia Geological Survey for encouragement and financial aid in support of this investigation. Dr. N. Gary Lane of the Department of Geology, Indiana University, kindly loaned me literature pertinent to this study.

My thanks go to Mr. Bruce Frumker for the photographs from which the illustrations were taken, and to my wife, Emily, for her aid in preparing the manuscript.

SYSTEMATIC PALEONTOLOGY

Class CRINOIDEA Miller, 1821

Family CATACRINIDAE Knapp, 1969

Genus DELOCRINUS Miller and Gurley, 1890

***Delocrinus segedii** sp. nov.**

Figs. 1-8

Diagnosis: Dorsal cup resembles that of *Delocrinus brownvillensis* Strimble, with subround to round outline in dorsal view, characteristic curvature of lateral walls, impressed primanal, and fine granulose ornament, but cup height shorter, basal impression deeper, basals extend higher on cup walls, and primanal smaller.

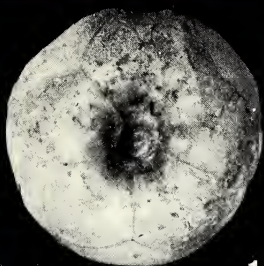
Types: Holotype CMNH 3847 (C radial damaged—restored); paratypes CMNH 3835, CM 33901 and CM 33902, all dorsal cups.

Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

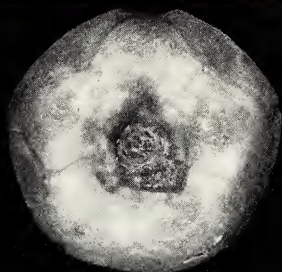
Localities: Holotype CMNH 3847 and paratype CMNH 3835 from road cut on south side of Interstate 70 and east of junction with Ohio Route 513, NW $\frac{1}{4}$ sec. 25 (lat 40° 03' 07" N., long 81° 19' W.) Oxford Township, near Middlebourne, Guernsey County, Ohio. Paratypes CM 33901 and

*Named for Mr. Robert Segedi, Science Instructor, Cleveland Museum of Natural History, who collected the Ohio specimens.

Figures 1-8. *Delocrinus segedii* sp. nov. Figs. 1-4 holotype CMNH 3847 (damaged C radial restored). Fig. 1, dorsal view. Fig. 2, posterior view. Fig. 3, anterior view. Fig. 4, ventral view. Figs. 5-8 paratype CM 33901. Fig. 5, dorsal view. Fig. 6, posterior view. Fig. 7, anterior view. Fig. 8, ventral view. All x 1.5.



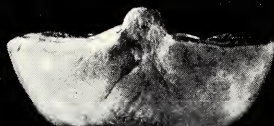
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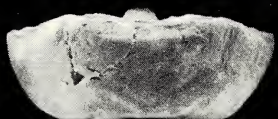
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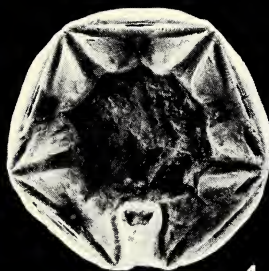
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CM 33902 from Tunnel Road Cut, West Virginia Route 67 (lat 40° 14' 24" N., long 80° 35' 53" W.) near McKinleyville, Brooke County, West Virginia.

Description: Dorsal cup of medium size, low truncate bowl-shaped, about $\frac{3}{8}$ as high as wide. Outline subround in dorsal view, pentagonal in ventral view. Height and width dimensions of basal impression less than half those of the cup. Stem cicatrix small. Infrabasals extend for slightly less than half the height of basal impression, steep walled proximally, sloping outward and downward distally, merging with slopes of basals without angularity. Basals with moderate downward slopes within impression, flattening, but still slightly concave at basal plane; distal slopes, along cup wall less steep, and gently convex. Tips of basals extend to about half the cup height.

Radials flare outward and upward, moderately convex longitudinally, less convex transversely. Forefacet very slight, broadly lunate. Transverse ridge and outward-facing lateral lobes visible in lateral view (barely showing in paratype CM 33901—result of compaction). Outer marginal ridge sags downward; broadly bowed in ventral view. External ligament pit slitlike, its outer ridge denticulate. Transverse ridge relatively delicate, denticulate, compressed adjacent to outer ligament pit. Lateral furrow moderately deep and broad, oblique ridge denticulate. Adsutural slopes low, but prominent, expanding widely toward body cavity, where high lateral lobes overhang them. Intermuscular notch broadly V-shaped, intermuscular furrow narrow, flanked by round-basined muscular areas.

Primalan concave from side to side in midregion; portion within the cup occupies a little less than a third of the cup height. Distally primalan slopes inward and upward; in holotype, distal facet shows small basin on each side of midline.

Ornament consists of fine granules, on primalan, radial and basal plates; not shown on proximal portions of basals of Ohio types (CMNH 3847 and CMNH 3835).

Measurements: Linear measurements in mm taken on holotype, CMNH 3847: Dorsal cup height, 8.7, width, 23.5, H/W ratio, 0.35; basal impression, height, 3.8, width 10.5; stem impression width 1.9; basal (EA) length, 9.6, width 9.4; radial (A) length, 7.8, width, 13.5; length suture between basals, 6.7; length suture between radials, 4.3; primalan height, 5.5, width 4.1.

Discussion: This species belongs to a *Delocrinus* lineage fairly well represented in Upper Missouri and Virgil sediments, characterized by dorsal cups showing granulose ornament and composed of rather massive plates which are easily damaged. The holotype, CM 3847, had most of the C radial broken away when found; the plate has been restored. Proximal portions of the basals and all of the infrabasals of the West Virginia paratypes were lost prior to deposition. I collected the latter specimens several years ago, but it was not until the better Ohio material was found that I felt that the species could be established securely.

Strimple (1949) pointed to the more rounded outline of the dorsal cup in dorsal view, coupled with the less angular longitudinal slopes of the basals, as characters distinguishing *Delocrinus brownvillensis* from *Delocrinus vulgatus*. These same features also appear to distinguish *Delocrinus segedii* from both *Delocrinus vulgatus* and *Delocrinus verus*. The height/width ratio is about the same for dorsal cups of the latter three species (about 0.35), but this ratio for *Delocrinus brownvillensis*, based on Strimple's values for height and width, is 0.39, rather than 0.35, the figure given by him. Height and width measurements of hypotype specimens of *Delocrinus brownvillensis* indicate even higher height/width ratios, up to 0.41 (Pabian and Strimple, 1973). The depth of the basal impression is less in *Delocrinus segedii* than in *Delocrinus verus* and *Delocrinus vulgatus*. The cup of *Delocrinus segedii* is ornamented; cups of *Delocrinus verus* and *Delocrinus vulgatus* are smooth.

Family LAUDONOCRINIDAE Moore and Strimple, 1973

Genus APPALACHIACRINUS* gen. nov.

Diagnosis: Dorsal cup low truncate bowl-shaped, nearly $2\frac{1}{2}$ times as wide as high. Outline irregularly hexagonal in dorsal view. Posterior interradius not impressed. Interradial notches faint. Infrabasals flat, basal and anal plates mildly convex, major portions of radials and first primibrachs swollen or bulbous. Ornament very fine irregular ridges. Infrabasal circlet very slightly upflaring, not visible in lateral view. Basals curve

*The generic name is in reference to the Appalachian region where the type species was found.

downward to basal plane, then upward along cup wall. Slight pits or impressions where distal extremities of basals meet corners of radials and anals. C radial widest, least convex, with distal slopes relatively gentle. Other radials more convex with distal slopes curving inward strongly. Radial articular facets peneplenary. Primalanal, secundanal and tertanal plates in the cup, in normal arrangement. First primibrachs spinose and axillary.

Type species: Appalachiocrinus erwini sp. nov., here designated.

Appalachiocrinus erwini** sp. nov.

Figs. 9-12

Diagnosis: As for the genus—see above.

Holotype: CMNH 3834, a dorsal cup retaining four first primibrachs.

Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

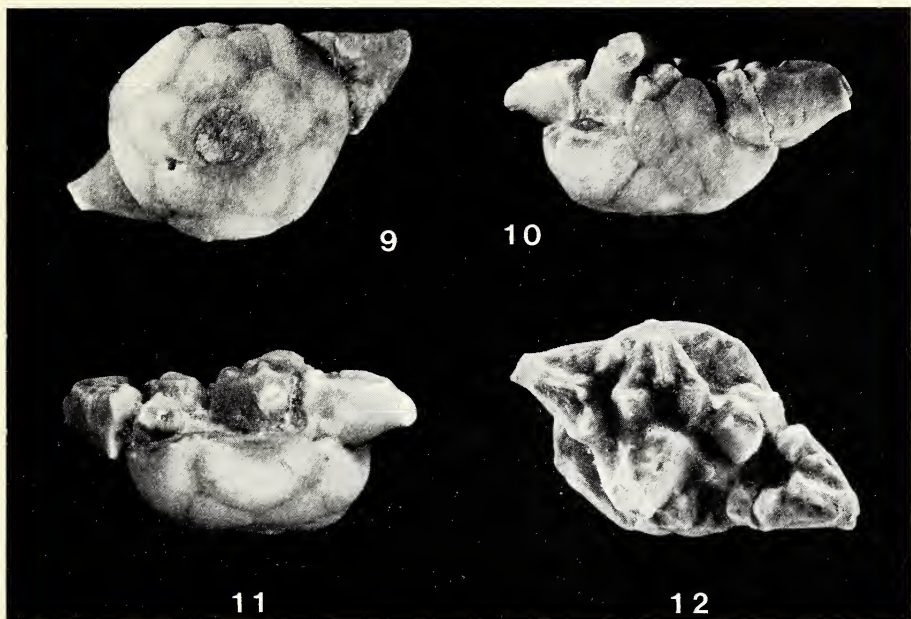
Locality: Tunnel Road Cut, West Virginia Route 67 (lat 40° 14' 40" N., long 80° 35' 53" W.) near McKinleyville, Brooke County, West Virginia.

Description: Dorsal cup low truncate bowl-shaped, nearly $2\frac{1}{2}$ times as wide as high ($H/W = 0.41$); outline irregularly hexagonal in dorsal view. Posterior interradius not impressed. Ornament very fine irregular ridges.

Infrabasal circlet nearly one-third diameter of cup, upflaring very slightly, not visible in lateral view. Stem wide, occupying most of circlet; closely surrounded by infrabasals. Infrabasals flat, with wide distal angles; distal surfaces flush with those of basals along common sutures. Basals gently convex, sloping downward from contact with infrabasals and then upward along cup wall. Slight pits where distal terminations of basals meet corners of radial and anal plates.

C radial widest and least convex of radial plates; distal slopes fairly gentle. Remaining radials bulbous; least convex from side to side; distal

**The specific name is in honor of Dr. Robert B. Erwin, State Geologist of West Virginia.



Figures 9-12. *Appalachiocrinus erwini* gen. et sp. nov. Holotype CMNH 3834. Fig. 9, dorsal view. Fig. 10, posterior view. Fig. 11, anterior view. Fig. 12, ventral view. All x 3.

slopes curving inward sharply in relatively broad areas defined by strongly arcuate forefacets. External surfaces slightly impressed in notches at summits of interradian sutures; articular facets peneplenary and moderately declinate. External marginal ridge bowed, sags downward and faces outward together with slitlike external ligament pit. Transverse crest low, denticulate; lateral furrows broad, shallow. Adsutural slopes gentle but extensive. Internal notch V-shaped; muscle area basins round.

Primanal, secundanal, and tertanal gently convex; arrangement normal. Two additional multifaceted anal plates present but dissociated.

First primibrachs axillary; all except B primibrach preserved. Plates spinose, major portion bulbous, not compressed from side to side. Spines arise high on plates, tips not preserved. Strong ridge separates right and left facetal areas. A single short secundibrach with part of articular surface facing outward rests on the dorsal faces of the secundanal and tertanal. It shows a wide V-shaped intermuscular notch and what appears to be a short intermuscular furrow flanked by shallow basins on each side.

Measurements: Linear measurements, in mm, taken on holotype, CMNH 3834: Dorsal cup height, 4.4, width 10.7; stem width, 2.2; infrabasal circlet width, 3.4, basal (AB) length, 2.8, width 3.5; radial (A) length 3.5, width 5.6; length suture between basals, 1.0; length suture between radials, 2.2; primanal length, 3.2, width 1.7; secundanal length, 2.9, width 2.3; tertanal length 3.0, width, 2.2; first primibrach (E) length along lateral suture, 2.5, width 4.9.

Discussion: This interesting little crinoid bears resemblances to *Laudonocrinus*, *Anchicrinus*, and *Athlocrinus*. The flat infrabasals and very slightly upflared infrabasal circlet are also features of *Laudonocrinus*, but *Appalachiacrinus erwini* differs from *Laudonocrinus subsinuatus* in not showing the infrabasals in lateral view. As in *Laudonocrinus*, the C radial is the widest and least convex, but the radials generally differ from those of *Laudonocrinus* in being for the most part bulbous, although steep walled distally. The axillary primibrachs are perhaps more like those of *Laudonocrinus* than those of any other laudonocrinid genus, but they are tumid and not compressed from side to side as in *Laudonocrinus subsinuatus*.

However, no other laudonocrinid genus approaches *Appalachiacrinus* in cup height. It resembles *Anchicrinus* and *Athlocrinus*, which have much shallower cups, in the convexity of its cup plates, in showing pits at the plate angles, and in the lack of an impressed posterior interradius, such as characterizes some species of the latter genera.

Family CROMYOCRINIDAE Bather, 1890

Genus PARETHELOCRINUS Strimple, 1961

***Parethelocrinus occultator** sp. nov.**

Figs. 13-15

Diagnosis: Cup less than three times wider than high, constricted at summit, basal impression shallow and wide, infrabasal circlet relatively large, downflaring. Sutures impressed, ornament finely granulose. Radials with prominent flat forefacets. Primanal, secundanal, and lower right corner of tertanal in cup, quartanal rests on secundanal, not in cup. Tertanal concealed by C ray primibrach.

*From the Latin *occultator* (concealer) in reference to the hidden tertanal.

Holotype: CMNH 3833, a crushed dorsal cup with three axillary primibrachs, one preserving portions of arms.

Referred specimen: CMNH 3802, associated cup and arm plates, including an axillary first secundibrach.

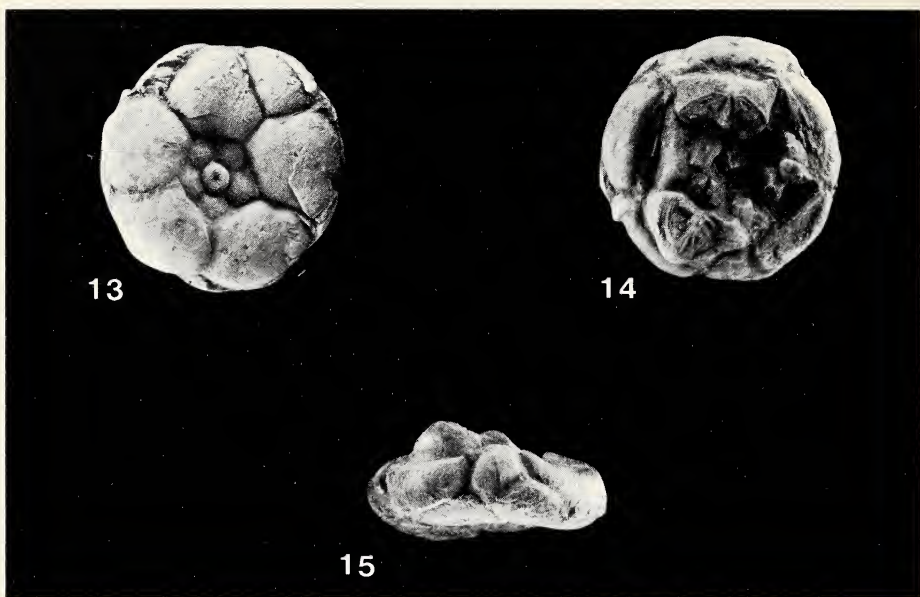
Occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

Locality: Tunnel Road Cut, West Virginia Route 67 (lat 40° 14' 24" N., long 80° 35' 53" W.) near McKinleyville, Brooke County, West Virginia.

Description: Dorsal cup low truncate globe-shaped. Cup of holotype crushed, but must have been less than three times as wide as high. Basal impression shallow and wide, infrabasal circle relatively large. Sutures between cup plates in shallow V-shaped impressions; ornament very finely granulose.

Stem prominent; infrabasals convex, downflaring. Basals gently convex within basal impression, with moderate outward and downward slopes to junction with radials; strongly convex beyond that region, curving abruptly upward along outer wall of cup. Radials moderately convex, widest at proximal lateral angles. Forefacets prominent in ventral view, flattened. External ligament pit slitlike. Transverse ridge of moderate height and denticulate. Internal notch V-shaped; intermuscular furrow narrow. Muscle areas with shallow curved grooves.

Three anal plates in cup. Primanal large, quadrangular; secundanal medium sized, pentagonal, its left side almost straight and nearly vertical in arrangement, meeting D radial and D primibrach; bears quartanal dorsally, extends in V-shaped angle to right, meeting with C radial above and making very wide contact with primanal below; narrow proximal side abuts against truncate CD basal. Surface exposure of quartanal slight, plate bent inward, expands laterally to left and right in direction of body cavity, contacts D first primibrach on left, firmly bound to tertanal at right. Sides of tertanal and quartanal directed inward on the right, bounding left side and corner of C primibrach. Tertanal sinks slightly below left lateral lobe of C radial and consequently is within cup, but entire plate would be concealed in external view if C first primibrach were in place. Distally, quartanal and tertanal bear facets for two additional tube plates. Another anal plate lies nearby in body cavity.



Figures 13-15. *Parethelocrinus occultator* sp. nov. Holotype CMNH 3833. Fig. 13, dorsal view. Fig. 14, slightly oblique ventral view. Fig. 15, posterior view. All x 1.

First primibrachs D, E, and A present; plates short in height, massive, showing prominent forefacets proximally and having rounded tips that project outward distally. Articular surfaces robust, transverse crests of both articular faces of the A plate very strongly and broadly denticulate, suggesting that this primibrach bore axillary secundibrachs. A single axillary secundibrach is associated with plates of the referred specimen, CMNH 3802, indicating that this species had more than 10 arms.

The E primibrach bore two arms; it retains a single first secundibrach of the left ray and three secundibrachs of the right ray. These plates appear to have attained biseriality on the second secundibrach. Isolated secundibrachs show flat lateral sides, prolonged in typical ethelocrinid fashion.

Measurements: Linear measurements, in mm, taken on holotype, CMNH 3833: Dorsal cup height, 13.0*, width, 34.0*; width stem, 4.0; width infrabasal circlet, 11.3; basal (EA) length, 11.9, width, 15.5; radial (E) length, 9.2, width (proximal lateral angle), 16.8, width (summit), 13.8;

length suture between basals, 8.7; length suture between radials, 4.6; primanal length, 12.0*, width, 11.0*, secundanal length 9.0, width 7.0*, quartanal length, 4.5, width 5.0+; axillary primibrach (A) length (along lateral suture) 5.0, width 13.8.

Discussion: In general, the dorsal cup of this species appears more like that of *Parethelocrinus magnus* (Strimple) than any other ethelocrinid species (cf Strimple, 1949, pl. 2, fig. 1, 3, 5, 6). The basal concavities and infrabasal circlets are much the same in the two species, and in ventral view the prominent flat forefacets of the radials are strikingly alike. Even the shallow grooves of the radial muscle areas appear the same in both taxa. *Parethelocrinus magnus* also shows an inward extension of the tertanal along the left lateral side of the C radial; this is the same region where the tertanal of *Parethelocrinus occultator* is found, but the tertanal and quartanal were not joined in the Strimple species and both plates articulated with the secundanal.

In a dorsal cup of *Dicromyocrinus geminatus* (Trautschold) figured by Yakovlev and Ivanov (1956, pl. 4, fig. 3) the tertanal occupies essentially the same position as in *Parethelocrinus occultator*, and probably would not have been visible in lateral view if the C primibrach were in place. However, in the Russian specimen, the tertanal is evidently a separate plate wedged in between the C radial and the secundanal. The quartanal is not shown. In the holotype of *Parethelocrinus occultator*, the quartanal and the tertanal are very closely joined and I cannot find clear evidence of sutural separation. If the two plates are fused, this may be an abnormal condition. On the other hand, the position of the tertanal is such that fusion with the quartanal would contribute to its function as a supporting plate.

*Estimated.

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A NEW SPECIES OF *PARALLELOCRIINUS* FROM THE VINLAND SHALE, PENNSYLVANIAN, OF KANSAS

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ABSTRACT

An inadunate crinoid, *Parallelocrinus mercenarius* sp. nov., from the Vinland Shale, Douglas Group, Virgilian Series, (Pennsylvanian) of Kansas is described. The species is distinguished by (1) a globe-shaped cup with round and shallowly scalloped outline in dorsal and ventral views; (2) a wide, steep-walled basal impression; (3) prominent basal plates with steep proximal slopes; (4) radials with proximal tips well above the basal plane; (5) hollows that border the plates extend to distal reaches of interbasal borders; and (6) distinctive rugose ornament. Comparison is made with two crinoid species from the Permian of Timor. Possibility of relationship to *Lopadiocrinus tuberculatus* Wanner is suggested. Close resemblances of species of *Parallelocrinus* to "*Delocrinus*" *rugosus* Wanner in external structures of dorsal cups are noted, but attributed to homomorphy; radial articular structure indicates that the Wanner species is referable to *Apographiocrinus*, consequently it is herewith designated *Apographiocrinus rugosus* (Wanner, 1916) comb. nov.

INTRODUCTION

The inadunate crinoid genus *Parallelocrinus* was proposed by Knapp (1969) having for its type species *Parallelocrinus typus* from the Burgner Formation, Atokan Series, of Missouri. Since then (Burke, 1971) I have attributed to the genus a second species, *Parallelocrinus sturgeoni* from the Ames Limestone, Conemaughan Series, of Ohio. In the present paper a third species, *Parallelocrinus mercenarius* sp. nov. from the Vinland Shale, Virgilian Series, of Kansas, is described.

I wish to thank Dr. Porter M. Kier and Dr. Richard E. Grant of the National Museum of Natural History, and Dr. Eugene S. Richardson, Jr. of the Field Museum for the privilege of studying specimens that were pertinent to this investigation.

I am also grateful to my wife Emily for arranging the illustrations for this paper, and to Bruce Frumker, Staff Photographer, for photographs from which the illustrations were made.

SYSTEMATIC PALEONTOLOGY

Class CRINOIDEA Miller, 1821

Family CATACRINIDAE Knapp, 1969

Genus PARALLELOCRINUS Knapp, 1969

Parallelocrinus mercenarius* sp. nov.

Figs. 1-4

Diagnosis: A species differing from *Parallelocrinus typus* and *P. sturgeoni* mainly in the following features: Dorsal cup more rounded in dorsal and ventral views and globe shaped, rather than bowl shaped, in lateral view, lateral walls showing greater curvature; base more sharply truncate; basal impression steeper walled and wider; basals more prominent in dorsal and lateral views, with steeper proximal slopes; proximal tips of radials arising higher on cup walls; hollows between plate borders extending beyond proximal tips of radials and entering slightly along borders between basals; depressions at proximal tips of radials shallower and broader; cup surface appears shaggy, showing distinctive rugose ornament.

Holotype: CMNH 3977, a dorsal cup lacking the infrabasal circlet.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

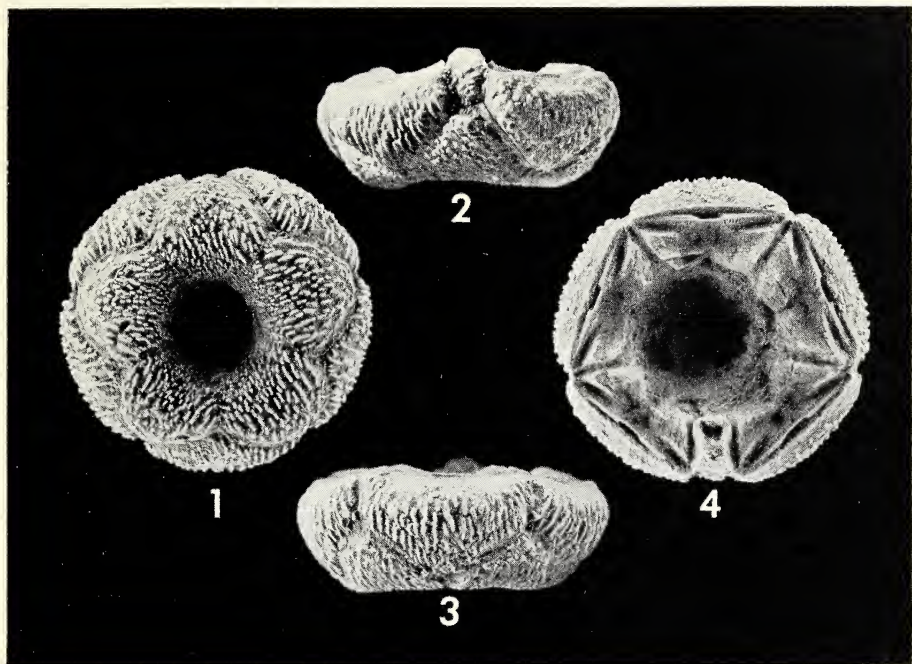
Occurrence: Vinland Shale, Stranger Formation, Douglas Group, Upper Pennsylvanian (Virgilian).

Locality: Homewood, Franklin County, Kansas.

Description: Dorsal cup $2\frac{1}{2}$ times as wide as high, and truncate low globe shaped; outline round and shallowly scalloped in dorsal and ventral views; right side of cup slightly higher than left. Basal impression steep walled and wide. Infrabasal circlet missing; height of impression unknown.

Basal plates downflaring steeply for most of their height within the basal impression, but bending rather abruptly outward on approach to basal plane; beyond basal plane plates slope gently outward and upward to their distal terminations.

*The holotype specimen was purchased from a dealer in geological supplies, hence the specific name. The specimen had been identified as *Graffhamicrinus magnificus* (Strimple).



Figures 1-4. *Parallelocrinus mercenarius*, sp. nov. Holotype, CMNH 3977, from the Vinland Shale, Douglas Group, Homewood, Franklin County, Kansas. Fig. 1, dorsal view; fig. 2, posterior view; fig. 3, anterior view; fig. 4, ventral view. X 2

Radial plates with proximal tips well above the basal plane and sloping upward and outward slightly steeper than basals to region of forefacets, where their surfaces curve inward, with gentler slopes, to summit of cup. Forefacets prominent, with depths about one-third those of the radial articular surfaces.

Radial facets face outward. Outer ligament ridge slightly arcuate, sags below transverse ridge; denticulate, at least in vicinity of slitlike ligament pit. Transverse ridge sharply defined, denticulate, contracts in vicinity of ligament pit, then expands on either side, but contracts again opposite inner reaches of lateral furrows, narrowing sharply to lateral extremities. Lateral furrows well defined, extend almost opposite extremities of ligament pit, flanked on inner side by steep-walled denticulate oblique ridge. Small central pit or foramen just below midline of transverse ridge on

inner side. Adsutural slopes steep; adsutural channels widening and deepening toward exits on internal side. Intermuscular notches broadly V-shaped. Intermuscular furrows short, angular, terminating between muscle areas. Muscle areas basin-like, separated also by rounded triangular area that expands upward, terminating below transverse crest opposite ligament pit.

Anal X convex from side to side, truncates distal tip of elongate CD basal, is impressed between C and D radials and extents for about a third of its height above the summits of those plates. It curves inward and upward, narrowing above, with concave lateral surfaces; distal articular surface faces both inward and upward and displays depressions on each side of the midline.

Wide hollows border sutures between cup plates, extending along interrarial sutures, sutures between radials and basals, and entering slightly along interbasal sutures. Hollows marked by smooth areas, shared by adjacent plates along interrarial and interbasal sutures; confined to basals along sutures between radials and basals. Distal tips of basals stand out in relief from floors of confluent hollows. Shallow depressions mark common sutures at proximal tips of radials, but small pits also present.

Ornament strikingly rugose, imparting shaggy appearance to cup; consists predominately of elongate ridges running parallel to length of plates (but opposite to length on anal X); ridges foreshortened or node-like within basal impression, on forefacet, and on anal X.

The cup shows evidence of damage by boring organisms. An ill defined subcircular depression with a central boss-like elevation, found near the tip of the EA basal, may represent the work of a gastropod. On the DE basal an elongate perforation is of the type usually attributed to the burrowing barnacle *Trypetesa*. Small round pits on the BC basal probably represent boring also.

Measurements: Linear measurements, in mm, taken on holotype CMNH 3977: Dorsal cup height, 8.0, width (max.), 20.0, H/W ratio 0.40; basal impression width, 8.9; EA basal length, 6.7 (appr.), width, 7.1; A radial length, 6.6, width 10.6; suture between BB, length, 4.9; suture between RR, length, 3.6; anal X height, 3.5, width, 2.7.

Discussion: *Parallelocrinus mercenarius* in several respects is more special-

ized than *Parallelocrinus typus* and *Parallelocrinus sturgeoni*. This is indicated by the steeper walled and wider proximal portion of the stem impression (and by inference a more robust stem); more prominent basals, having steeper proximal slopes; proximal tips of radials arising higher on the cup walls; presence of shallow depressions where the proximal tips of the radials meet subjacent basals; and hollows between plates prolonged slightly, extending to distal reaches of interbasal borders.

The peculiarities which I noted previously (Burke, 1971, p. 201) as characteristic of *Parallelocrinus*, notably "... the distal portions of the basals standing out in relief, with their tips elevated above the hollows" are also to be found in at least two specimens of crinoids from the Permian of Timor. The one, *Lopadiocrinus tuberculatus* Wanner (1937), not only shows the features noted above, but also essentially all of the distinctive surface structures of the cups of *Parallelocrinus*, including the deep forefacet, although the hollows between the plates are evidently more deeply entrenched and extend along the interbasal borders to merge with the basal impression. The radial articular facets are similar to those of *Parallelocrinus* and other Catacrinidae. It must be granted that the prominent asymmetrical infrabasal circle and shallow basal impression would seem to exclude derivation of *Lopadiocrinus tuberculatus* from any known species of *Parallelocrinus*, but the possibility of descent of the Wanner species from *Parallelocrinus* or a *Parallelocrinus*-like ancestor deserves consideration.

In over-all external structure of the dorsal cup, the most striking similarity to species of *Parallelocrinus* is found in the Timor species originally described as "*Delocrinus*" *rugosus* by Wanner (1916). I have seen a specimen of this crinoid, USNM S3982, which is preserved in the Springer Collection of the National Museum of Natural History. It is labeled *Ceriocrinus rugosus* Wanner, and was probably identified by Wanner himself. In this Timor species we again find the distal reaches of the basals standing out in relief, and the hollows have the same distribution as in *Parallelocrinus* except that as in *Lopadiocrinus tuberculatus* they also parallel the interbasal sutures, terminating at the basal impression, just above the basal plane. The basal impression is moderate; it resembles that of *Parallelocrinus mercenarius* in being steep walled and relatively wide. The forefacet is prominent and deep. Anal X barely nicks the summit of the dorsal cup; it is wedged in between the shoulders of the C and D radials; below it is separated from the top of the CD basal

by these posterior radials, which have a common lateral suture. This is similar to the structure and disposition of the plates in the posterior interradius of *Parallelocrinus sturgeonii*, except that in that species, anal X and the CD basal are only slightly separated. Even the dorsal-cup ornament of USNM S3982 somewhat resembles that of *Parallelocrinus mercenarius*; the rugae, although coarse, are oriented much as are the more slender ridges of the latter species.

However, the articular surfaces of the radials of USNM S3982 are definitely indicative of *Apographiocrinus*; two of the interfacet "prongs" discussed by Moore and Plummer (1940, p. 117) are preserved in entirety, and it is evident that they are merely exaggerations of the same structures found in American species of the genus. It follows that the remarkable correspondence in surface structures of the dorsal cups of species of *Parallelocrinus* and those of Wanner's "*Delocrinus*" *rugosus* is quite evidently attributable to homeomorphy, and is not indicative of any close relationship between Wanner's species and representatives of *Parallelocrinus*.

As noted previously, Wanner first described this species (1916) as *Delocrinus rugosus*, then (1942) attributed it to *Ceriocrinus*, and finally (1949) redescribed it as *Graphiocrinus?* *rugosus*. I am herewith designating it *Apographiocrinus rugosus* (Wanner, 1916) comb. nov. This adds a third species of *Apographiocrinus* to the Timor fauna; Moore and Plummer (1940) also placed *Graphiocrinus quinquelobus* Wanner and *Delocrinus pumilus* Wanner in synonymy under *Apographiocrinus*.

Moore and Plummer (1940) having relegated *Poteriocrinus rugosus* Shumard (1858) to synonymy under *Delocrinus*, argued (1940, footnote p. 272) that "*D. rugosus* Wanner, 1916 is a homonym of *D. rugosus* (Shumard) 1858 . . ." Inasmuch as Shumard's type was never illustrated and is no longer in existence, there is no way of determining what its generic affiliation may have been, and in any case there would now seem to be no grounds for applying a new trivial name to *Apographiocrinus rugosus*.

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A NEW PERMIAN *CIBOLOCRINUS* FROM BOLIVIA

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ABSTRACT

A flexible crinoid, *Cibolocrinus patriciae* sp. nov. from the Permian Copacabana Group of Bolivia is described. The holotype specimen was found at the original D'Orbigny collecting site near Yaurichambi, 10 km east of Lake Titicaca. The species is distinguished principally by the upflaring infrabasal plates, which are slightly convex, show impressed sutures, and are visible in lateral view of the dorsal cup. An inadunate crinoid from the same locality, previously described as *Delocrinus titicara* by Strimple and Moore, is here designated *Endelocrinus titicara* (Strimple and Moore, 1971) comb. nov.

INTRODUCTION

In 1969 Drs. Frank Stehli and James Helwig of Case Western Reserve University conducted a field study of Carboniferous and Permian strata of Bolivia. Mrs. Patricia Helwig accompanied the party as a representative of the Cleveland Museum of Natural History. The party visited the locality in the vicinity of Yaurichambi, 10 km east of Lake Titicaca, where D'Orbigny (1842) made the initial collection of Permian fossils from Bolivia. At that place Patricia Helwig collected fossil invertebrates from the Copacabana Group (Wolfcampian) and found a specimen of the flexible crinoid *Cibolocrinus* that proves to be a new species, which is described in the following pages. A paper by James Helwig (1972, map, fig. 1; Yaurichambi section, fig. 2) shows the location of Yaurichambi and a stratigraphic section taken at the collecting site.

Previously (1971) Strimple and Moore, in the first formal description of a crinoid from the Bolivian Permian, proposed the name

Delocrinus titicara for an inadunate crinoid that was also derived from the Copacabana Group at the Yaurichambi locality. However, their holotype specimen shows pits at the corners of the dorsal cup plates and the arms attain normal biseriality well above the summits of the primibrachs. These are diagnostic features of the genus *Endelocrinus* Moore and Plummer, 1940. In consequence I am herewith designating the taxon *Endelocrinus titicara* (Strimple and Moore, 1971) comb. nov. Further discussion of this species is reserved for a future publication.

Other references to Permian crinoids of Bolivia are few. Ahlfeld and Braniša (1960, p. 104) listed Icthyocrinidae indet., *Lecythiocrinus* cf. *olivaeformis** and *Delocrinus* sp. from the Cocacabana Group at Lake Titicaca and Yaurichambi, and from the same beds at Zudáñez, *Delocrinus* sp. and *Aulocrinus*? sp. Of the latter, which is figured (ibid. pl. 7, fig. 20) Webster (1970) notes "(probably not an *Aulocrinus*)"; judging from the illustration, I take the specimen to be a cromyocrinid. In another publication Braniša (1965, pl. 54) illustrated additional crinoid material from the Copacabana, including *Lecythiocrinus* cf. *olliculaeformis* from Zudáñez (fig. 19), part of a biserial arm from Yaurichambi (fig. 43), and portions of crinoid stems (figs. 1-27), from Zudáñez, Apillipampa, Colquenchá, and Yaurichambi.

ACKNOWLEDGMENTS

For the privilege of studying comparative material in their care, I am indebted to Drs. Porter M. Kier of the National Museum of Natural History, Stig Bergström of the Orton Museum, Ohio State University, and Eugene S. Richardson, Jr. of the Field Museum. Dr. G. D. Webster of Washington State University furnished bibliographic data and Dr. James Helwig of Case Western Reserve University loaned me literature pertinent to this study. I thank my wife Emily for preparing the illustrations, and Bruce Frumker, Staff Photographer, for making the photographs from which the illustrations were made.

*Evidently a *nomen nudum*

SYSTEMATIC PALEONTOLOGY

CLASS CRINOIDEA Miller, 1821

Family MESPILOCRINIDAE Jaekel, 1918

Genus CIBOLOCRINUS Weller, 1909

*Cibolocrinus patriciae** sp. nov.

Figs. 1-5

Diagnosis: Walls of dorsal cup outflaring from base, but more erect in region of radial circlet. Infrabasals visible in lateral view upflaring, and convex, with sutures between them impressed. Basals elongate, with sharply angular tips and straight distal borders.

Holotype: CMNH 3801, a mashed dorsal cup with complete B and C and damaged A and D IBrr.; also damaged A and B IBrr.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

Occurrence: Copacabana Group, Lower Permian (Wolfcampian).

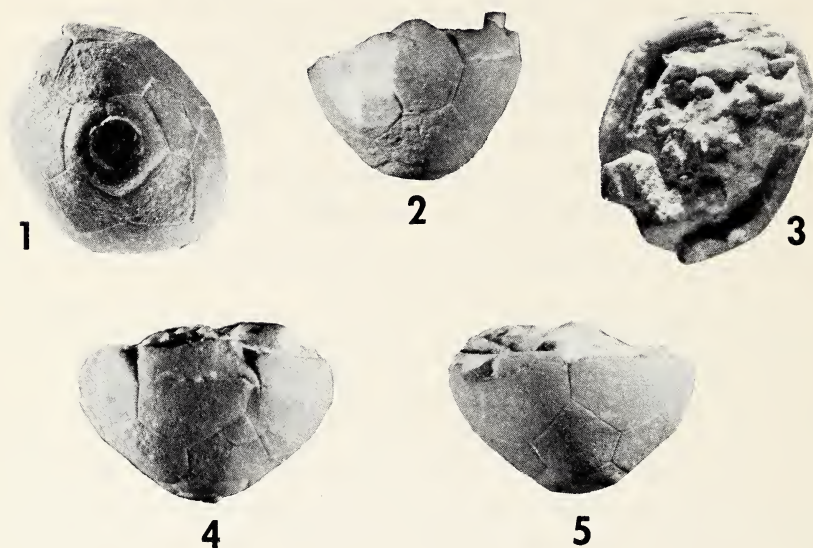
Locality: Hogback called "Cerro Vacha Kahtawi"; 3 km WNW of village of Yaurichambi and 10 km east of Lake Titicaca, just south of small church school (lat 40°17'56" S., long 68°29'10" W.) northern Bolivia.

Description: The dorsal cup is mashed and it is difficult to get a clear concept of its original proportions. The portion in the vicinity of the E ray seems to be the least distorted. Apparently the cup was low bowl shaped, and probably a little less than twice as wide as high. In lateral view the walls flare outward from the base, becoming steeper and more rounded a little above midheight. The posterior slope was evidently gentler than the anterior. In dorsal or ventral view the cup was probably pentagonal in outline.

The three infrabasals are clearly upflaring in lateral view of the cup. They are slightly but definitely convex, most so longitudinally, and a little indented along their common sutures. The A-ray plate is the smallest of the three. Part of the stem, showing a round lumen, is preserved. Its impression occupies nearly 3/5 of the diameter of the infrabasal circlet.

The five basals are slightly convex, with short interbasal sutures.

*The species is named for Patricia Helwig.



Figures 1-5. *Cibolocrinus patriciae* sp. nov. Holotype, CMNH 3801 from the Copacabana Group, Lower Permian, near Yaurichambi, Bolivia. Fig. 1, dorsal view; fig. 2, posterior view; fig. 3, ventral view; fig. 4, C-ray view (primanal at left); fig. 5, EA-interray view. X2

Their slopes are moderate. Except for the CD plate, each is hexagonal and extended distally, having a sharp tip. Their proximal angles are quite broad; that of the CD basal is least so. All of these plates are wider than long, including the CD basal, but the latter is the largest, with greatest distal extent. The CD basal is also heptagonal, being truncated distally where it meets the primanal plate.

The A, B, and E radials are about $3/5$, but the C and D radials are only slightly more than $1/2$, wider than long. The interrarial sutures are nearly as long as the interbasal sutures, but the radial-primanal sutures are half again as long. The radials are slightly convex longitudinally and transversely, but are more erect than the basals, and the cup walls are perceptibly steeper in the region of these plates. Interrarial notches are present at the summits of the radials. The articular surface of the E radial is exposed, revealing the typical

Cibolocrinus structure, with fan-shaped depressions at the lateral extremities and the surface contracted medially opposite the slitlike ligament pit.

The primanal is a large plate, nearly as long as the CD basal and a little more than half as wide. More than half its height is below the summits of the posterior radials. The plate is heptagonal; it has been damaged distally, but still shows four facets above the radials. Laterally it is notched in areas adjacent to the summit regions of the C and D first primibrachs.

Only portions of the A and D first primibrachs are preserved, and they show no details of the articular surfaces. The shattered E first primibrach was removed to expose the articular surface of the underlying radial. The C first primibrach is entire, and the adjacent B plate is essentially complete also. At midwidth these plates are about as long as the interrarial sutures, but they are longer laterally, where they project downward along the interrarial notches, although there is some distal increase also along the sides of the C plate, and the right side of the D plate shows marked elevation. The distal articular surface of the C first primibrach shows a slitlike external ligament pit, similar to that of the radial, but the lateral depressions are deeper and more basin-like than those of the radial. These plates bear notches that extend below their lateral summits (similar notches are found on the primanal, as noted above). Lateral extension of the second primibrachs extended downward along these notches.

Part of the articular surface of the left side of the B second primibrach is preserved; the lateral depression is similar to that of the first primibrach, although shallower. The remainder of this second primibrach is shattered and crushed. The adjacent A second primibrach is also too distorted by crushing to yield reliable data.

The cup surface appears finely granulose, but the ornament is not clearly distinguishable.

Measurements: Linear measurements, in mm, taken on holotype, CMNH 3801: Dorsal cup height, 8.5 (est.), width 16.0 (est.); H/W ratio, ca. 0.53; stem impression width, 3.9; infrabasal circlet width, 6.8; basal (EA) length, 5.4, width 5.8; radial (E) length, 4.9, width, 8.6; length suture between basals, 2.2; length suture between radials,

2.0; primanal height, 5.2 (appr.), width, 4.8.

Discussion: *Cibolocrinus patriciae* resembles certain Pennsylvanian representatives of the genus to the extent that its infrabasal plates are visible in lateral view of the dorsal cup. In the Morrowan *Cibolocrinus circulus* the lateral exposure of these plates is much less than in *C. patriciae*, and the cup outline has been described as "... subhemispherical when viewed from the side" (Moore and Strimple, 1973, p. 33). Although in its proximal half the cup of *C. patriciae* flares outward from the base, it is steeper walled and slightly rounded distally, thus differing from *C. circulus* and from the Missourian species *C. erectus* Strimple, 1951a and *C. conicus* Strimple, 1951b. In both of the latter forms the cup walls flare outward strongly from base to summit, and the dorsal cup has less height than that of *C. patriciae*, which in turn is surpassed in height by the cup of *C. circulus*. *Cibolocrinus patriciae* shows greater exposure of the infrabasal plates in lateral view than we find in Strimple's taxa, along with somewhat greater width of its infrabasal circle and slightly greater diameter of the stem impression. Among all four species, *C. patriciae* is unique in displaying convex infrabasals with impressed sutures. The elongate basals of *C. patriciae* compare to some extent with those of *C. circulus*, but in *C. circulus* the distal borders of the basals are curved, rather than straight. The interradian notches noted by Strimple in *C. erectus* are present in *C. patriciae*; they are also apparently present in *C. conicus*, but seem to be absent in *C. circulus*, which would be consistent with Strimple's (1951a) observation of their absence in Morrowan forms.

In competition with species of *Cibolocrinus* having flat-based dorsal cups, these forms with upflared infrabasals may have had the advantage of offering less resistance to strong water currents, and thus might have survived under conditions where species with the more specialized type of cup could not. There is insufficient evidence to support the argument that species of *Cibolocrinus* showing upflared infrabasals are examples of regressive evolution. Already present in Lower Pennsylvanian time, species with infrabasals of this type probably occupied an environmental niche where this feature was an advantage, and they persisted into the Lower Permian with little further specialization.

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SOME MISSISSIPPIAN CERAMICS FROM ARKANSAS, IN THE CLEVELAND MUSEUM OF NATURAL HISTORY

DAVID S. BROSE

The Cleveland Museum of Natural History

with

AN ANALYSIS OF THE CARBONIZED PLANT REMAINS

RICHARD I. FORD

Ethnobotanical Laboratory, University of Michigan

ABSTRACT

Reanalysis of Cleveland Museum of Natural History collections has revealed evidence for an early agricultural occupation of an archaeological site in northeastern Arkansas. This Mississippian culture mound, dated to A.D. 1050, showed distinctive ceramics with ethnobotanical material suggesting a revision of earlier theories of prehistoric diffusion in the eastern United States.

During December of 1973, as part of my duties as Curator of Archaeology for The Cleveland Museum of Natural History, I assisted in the transfer of a considerable amount of archaeological and ethnological material from a soon-to-be demolished storage building into the Museum's permanent research collections. Much of this material had been donated by private parties during the nineteen thirties, and had been accessioned prior to 1936. It was never really looked at by any professional archaeologist until the spring of 1974.

In one large cardboard box, taped shut, and located in a deep storage midden in a back closet, were two shell-tempered, looped-handled bowls: a large intact bowl (fig. 1) with an average lip thickness of about 4.7 mm ($s^2 = 1.9$ mm) and a smaller, similar partially

reconstructed bowl (fig. 2) with an average lip thickness of 3.9 mm ($s^2 = 1.8$ mm). The smaller vessel has traces of red fugitive slip. The vessels both bore the C.M.N.H. catalog number 9674. References to the accession catalog indicated only that the two vessels were from Cross County, Arkansas, and had been donated together to The Cleveland Museum of Natural History by a Mr. H.P. Shaw some time between 1927 and 1932. Interesting, but not really significant.

Working with a graduate assistant during February of 1974, I continued sorting through the older materials. Within a large cardboard box marked as coming from a mound on Weeden Island in Tampa Bay, and containing a series of shell (*Busycon?*) implements, fragments of human skeletal material, and a few Franklin Plain and Carabelle Incised sherds (Willey 1949:v.113, p.479) was a small metal box about 9 x 4 x 2 inches rusted shut. Inside this small metal cigarette or cigar box were three ceramic sherds, a series of botanical materials including nut shell, maize cob, various seeds which I could not recognize even to family, and several pieces of wood fiber about 3 inches long and approximately 3/4 inches in diameter. Several of the latter appeared to have been varnished. Included within the metal box was a worn, folded, and somewhat rust-stained note, which reads:

9674

— Two pots and seeds

acca; H.P. Shaw

collected by — Jones [1 — 7] below ground at More's Md. about four miles S. of Parkman in Cross Co., Arkansas on E. Side of the river.

These pots were found together and were dug out w— the seeds and shavings in the bigger pot made of mixed clay and [clam] shells. The small clay shards were found under these pots and the big broken shard with lines scratched was in the dirt above.

While there is a village named Parkman in Ohio (about 25 miles ESE of Cleveland) there is only a Parkin in Cross County, Arkansas. While there are several rivers in Cross County, there is only one major one: the St. Francis. While C.B. Moore operated upon local mounds, the only mound he reported which was about four miles south of Parkin on the east side of the St. Francis was the *Rose Mound* (Moore, 1910 :276-303). The note in *The Archaeological Survey of the Lower Mississippi Valley* (Phillips, Ford and Griffin, 1951 :278) that Rose had been severely potted since Moore's day lent some support to the notion that The Cleveland Museum of Natural History had obtained material probably assignable to the Rose Mound.



Figure 1. Large shell-tempered vessel probably of Mississippian Plain type, Mound Field variety, within which the carbonized botanical remains were found. CMNH Accession No. 9674.



Figure 2. Small red-slipped vessel (partially reconstructed) of Old Town Red type, associated with the large bowl within the mound. CMNH Accession No. 9674.

The two undecorated small rimsherds in the metal box were clay or grog tempered and can probably be considered representative of some variant of Baytown Plain (Phillips, Ford and Griffin, 1951 :270). Both of these rimsherds have a relatively thin lip thickness (\bar{x} = 9.0 mm) and display a hard compact paste. They seem equivalent to what Phillips (1970:57) has called the *West Lake* variety of Baytown Plain. The larger sherd was coarsely shell-tempered as were the two complete vessels. It is not a complete rim but probably comes from just below the lip—it is broken along a medium wide incised line. Below this break are two parallel horizontal (?) incised lines about 1.5 mm wide, 0.8 mm deep, and 8.8 mm and 9.2 mm apart. Below these the sherd curves out toward the shoulder and is roughly broken about 17 mm below the lowest incised line. This neck sherd has a very Coles Creek look although if it truly overlies the Neeleys Ferry Plain vessels that would suggest a stratigraphic problem. A more reasonable attribution may be suggested, however, as Coles Creek is not generally found as far north as Cross County, Arkansas (J.B. Griffin: personal communication). This sherd can easily be encompassed within what Phillips has characterized as the Mound Place variety of the type Mound Place Incised (Phillips, 1970: 135, fig. 59c).

There is little question that the two complete shell-tempered vessels with loop handles can be considered some variety of Neeleys Ferry Plain (Phillips, Ford and Griffin, 1951 :287). These Mississippian Plain vessels do not appear quite thin enough to meet Williams (1954) or Phillips (1970:132) criterion for Mississippian Plain, var. Coker. They both might fall within what Phillips would consider Mississippian Plain, var. Mound Field although adequate quantified data for certain attribution are not presented in that monumental report (Phillips, 1970:132-3). The smaller vessel with traces of red slipping should thus represent an example of Phillips' Old Town Red, var. Old Town (Phillips, 1970:145).

On both of these vessels, the paired loop handles are undecorated and are diametrically opposed on the vessels. The lower loop end is riveted through the vessel wall and luted on the interior. The upper handle end is attached by luting on the rim at the lip. On both vessels the loop handles rise slightly higher than the rim itself although erosion and breakage along much of the vessel rim make any more quantified statement spurious. These loop handles are virtually identical to one illustrated by Phillips, Ford and Griffin (1951 :228) which came from

the lower levels of the Rose Mound. They are similar to the loop-handled Neeleys Ferry Plain vessels reported from the early Mississippian Banks Mound 3 dated A.D. 1075 ± 75 . Similar vessels formed part of a richer ceramic assemblage with dates of A.D. 710 ± 150 , A.D. 930 ± 150 , and A.D. 1100 ± 110 in Crittenden County, Arkansas (Perino, 1967:69).

The wood shavings from the large pot were identified by Dr. O. Elzam of the Case Western Reserve University Biology Department as most likely some non-twigg portion of *Carya*, possibly *ovata*. I shaved off all the varnished surfaces and ended up with a handful of match-stick-sized fragments. These were then washed with a variety of solvents, washed with acid and base, and rewashed several weeks with distilled inert water by Dr. A. Sumodi of the C.W.R.U. Radio-carbon Lab. These wood fragments were then combusted and the carbon content converted to benzene, and the C^{14} content counted. The resultant date (CWRU-172) is A.D. 1050 ± 65 or BP 900. Until this date was returned it was uncertain whether the wood represented some rather recent contamination, or whether the association reported on the C.M.N.H. accession note was valid. It now appears most reasonable to assume that the date on the wood shavings also refers to the ceramics within which Mr. Jones claimed to have found them.

This suggests that the other ethnobotanical materials can also be referred to an early Mississippian period of A.D. 900-1100, and that there might be some value in obtaining the evaluation of a competent ethnobotanist concerning their specific identification and significance. Dr. Richard I. Ford of the University of Michigan Museum of Anthropology Ethnobotanical Laboratory was kind enough to consent to analyze these materials. His description and discussion are appended to this report.

Before beginning any extended discussion on the archaeological significance of these rediscovered ceramics and their contents, it is necessary to inquire more closely as to their context. Dr. J.B. Griffin (personal communication 21 May 1974) has pointed out that there is

...very little control over the time at which the seeds and shavings were utilized or how they got into the vessel. While it is not unreasonable to suggest that the site could be the Rose Mound, I would say that if the gentleman went by road from Parkin to the site that it would not be much more than two miles but if he went by water it would be probably closer to four miles. Down river from the Parkin site there is another site (12-N-6) which we identified as the Westmorland site. I don't see how you could be sure what site these materials come from.

In addition to Westmorland, the Lower Mississippi Valley Survey also identified the Welshans Place site (12-N-5) also on the east side and about two miles further down river from the Westmorland site. The Westmorland site however yielded only scanty amounts of middle Baytown ceramics (Phillips, Ford and Griffin, 1951: fig. 20) while the Welshans Place site, aside from lying beyond the 4-mile limit was apparently neither visited by Moore (Moore 1910), nor contained any ceramics which predated the early Mississippian horizon (Phillips, Ford and Griffin, 1951: fig. 20). The Rose Mound site not only produced materials from late Baytown through late Mississippian, but gave evidence of an early Mississippian component with shell-tempered plain ceramics which differed somewhat from typical Neeleys Ferry Plain (Phillips, Ford and Griffin, 1951: 105-110, 287-88; Phillips, 1970:933). As Phillips (1970:246) later noted,

In a large surface collection from the Rose Mound (12-N-3) made in 1940, there were only five clay-tempered sherds out of a total of 1416 (Phillips, Ford and Griffin 1951: fig. 21, sample no 12-N-3/A). A later test excavation in 1947 revealed a 100% pure 'clay-tempered' component with sherd yield per level as high as those in the overlying shell-tempered levels and plow-zone (*ibid.* fig. 53)

Given available information, it seems quite reasonable to accept the information in the C.M.N.H accession note accompanying the ethnobotanical material and the three sherds in the metal box. The stratigraphic sequence thus indicated would suggest a late Baytown component overlain by an early Mississippian occupation with plain loop-handled vessels dated at A.D. 1050 ± 110 , below incised Mississippian Ceramics. This sequence certainly conforms to the earlier ceramic chronology developed by Phillips, Ford and Griffin (1951) and should be capable of being placed within the more detailed framework recently proposed by Phillips (1970). If there are indeed sequent occupations, the only ceramics which can be assigned to a particular phase would be the Mississippian Plain (var. Mound Field, and var. Old Town) bowls. These could easily represent a portion of Phillips' revised Parkin Complex, the absence of Parkin Punctate and Barton Incised being the result of sampling error. With the association of the radiocarbon of A.D. 1050 ± 110 these shell-tempered vessels would fall into the Cherry Valley Phase (Phillips 1970, 930-33). While this date may seem somewhat early for Mississippian Plain ceramics in the St. Francis area it agrees with Perino's dates at

Cherry Valley and Banks (Perino, 1967:67). Phillips, discussing this Cherry Valley phase, has predicted that as new data continue to accumulate, such dates will seem less a special case (1970:930).

It is not, unfortunately, certain from the Cleveland Museum's note of Mr. Shaw's recollection of Mr. Jones' report, that three distinct components are indeed present. Phillips (1970:914), following earlier suggestions by Williams for southeast Missouri, recognizes a late pre-Mississippian Black Bluff horizon marked by a plain "clay-tempered" ware with a harder, more compact paste than is normal for Baytown Plain in this region. Indeed, Phillips suggests two distinct late Baytown phases flanking the lower St. Francis area, both characterized by a preponderance of Baytown Plain with Coles Creek "earmarks." Phillips (1970: 916-17) cites Hester Davis's 1967 characterization of the Toltec phase occupying the area between the St. Francis and the Mississippi as containing components with Mississippian settlement patterns associated with clay-tempered Baytown and shell-tempered Mississippian Plain ceramics.

If the materials herein described from the Cleveland Museum which are tentatively assigned to the Rose Mound site represent the ceramic assemblage from a single occupation, their relative stratigraphic occurrence within the component may be considered unimportant. In that case they should probably be assigned to this Toltec phase. In this event the radiocarbon date of A.D. 1050 \pm 110 should represent a reasonable (if not conservative) temporal position for the early Mississippian transition in the St. Francis basin. Phillips has pointed out (1970 :960) that the present state of calendrical dating in the lower Mississippi valley need not be taken too seriously in its present state of development. He postulates the first appearance of Mississippian ceramics in the Yazoo region (at about A.D. 1000) in his Crippen Point Phase (1970 :fig 450A). This suggestion has received some support from the recent excavations at the Winterville site in the Yazoo basin where Brain has recovered Mississippian ceramics late in a Crippen Point phase dated A.D. 1050-1200 (Brain, 1970: 276,304). While one might presume that such ceramics would be earlier upstream, it seems preferable at this point to accept Phillips' (1970:930) cautious prediction that,

As other early Mississippi data accumulate, as they are bound to do, . . . it may turn out that Mississippian Culture was developing over a broad front with interconnections that were not exclusively in a one-way, north-south direction.

CARBONIZED PLANT REMAINS FROM CROSS COUNTY, ARKANSAS

Museums are fascinating places. Their lure captivates the dreams of children and stimulates the imagination of adults. But to the scientist they are the foster homes of displaced discoveries. It is only in their confines that the archaeologist can reexamine the excavated artifacts of a predecessor and more often than not "excavate" once again long forgotten and unreported relics of man's prehistoric past. Such was the fortuitous discovery by Dr. David S. Brose of The Cleveland Museum of Natural History when he salvaged from an old museum warehouse an unpublished Neeleys Ferry Plain vessel containing several carbonized plant fragments. They were submitted to the Ethnobotanical Laboratory for identification.

While these charred remains are an unrepresentative sample of the plants used by early Mississippian peoples, nevertheless they do contribute to an accumulation of similar data that together are enlightening our knowledge of subsistence patterns 1000 years ago.

In his report Brose documents the inadequate records accompanying these plant parts. It is evident that they do come from a mound located south of Parkin in Cross County, Arkansas. Whether the actual site situated on the east side of the St. Francis River was the famous Rose Mound remains uncertain.

The remains consist of two butternut shells, one pawpaw seed, three bean cotyledons, three kernels of corn, and three pieces of cobs. Why they were in this pot is not clear; perhaps their excellent state of preservation attracted the attention of the excavator and he placed them there out of harm's way.

The two nut shells, weighing 3.3 g, are butternuts, *Juglans cinerea* L. From a phytogeographical point of view this is an interesting identification. Butternuts are common throughout the midwest, including southeastern Missouri, but are rare in Arkansas. Aside from two or three disjunct populations their main occurrence in this state is along the riverbottom and alluvial benches of the St. Francis River. Here butternuts are a common element in the bottomland hardwood forests. This archaeological find supports the hypothesis that the modern pattern of distribution existed in the early part of the tenth century A.D. as well.

The nut, an ovoid fruit 50 to 80 mm long, ripens in September and

October. It contains a good vegetable protein and is an excellent source of protein but does not store well for long periods of time without becoming rancid. As a consequence it may have been necessary to process these tasty nuts soon after they ripened by removing the thin hull and extracting the meat from the cracked shell. The oil could be separated from the meat by boiling. Butternuts undoubtedly contributed only a minor portion of food to the prehistoric diet. The trees are rarely found in groves, most often singly, and each mature tree produces a good crop of nuts every second or third year at most. A thrifty tree yields only 1/4 to 1 bushel of nuts (Fowells 1965:208-10). Unless simultaneous access to many trees is available, a family, much less a village, would benefit little if it attempted to rely on butternuts.

The pawpaw, *Asimina triloba* L. is another component of bottom-land vegetation although it will also occur as a mature fruit-bearing tree in later stages of old field succession. The fruits ripen in the early fall and are a delightful treat. The evidence for their consumption at this site is represented by only one seed measuring 22 mm in length and 11 mm in width. It is well within the range of modern examples. Pawpaw seeds have been identified from a number of Mississippian sites, including the neighboring Parkin Site (Cutler and Blake 1973:9-10).

Beans and corn represent the only evidence of cultivated plants. The three beans, *Phaseolus vulgaris* L., are all broken. The most complete measures 10 mm by 6.2 mm. The remainder have widths of 6.7 mm and 5.6 mm; their lengths are indeterminable.

Beans are not found in every excavation of Mississippian sites, and actually they may not have been grown by every community. They were a late introduction into the eastern United States, perhaps reaching this area as late as A.D. 900. Long recognized for their protein content and complementary relationship with corn's amino acids, they were not essential to the Mississippian economy everywhere. Other native foods such as acorn (Wilma Wetterstrom, personal communication) have a lysine value that will bolster the nutritional value of corn as well.

The fragmentary condition and small sample of corn permits only a superficial discussion. We know that ethnographic cultures living in the Southeast raised a number of varieties of corn, but to date the phenotypic traits used to define these types have not been distin-

guished for analyzing carbonized archaeological remains. Therefore our categories are artifacts of limited analytical procedures.

The three kernels of corn are similar in size and shape. Although two kernels are lacking their "germ," all have a crescent outline and are wider than they are high (width x height: 11 x 7.9; 7.9 x 6.2; 9.2 x 7.3 mm).

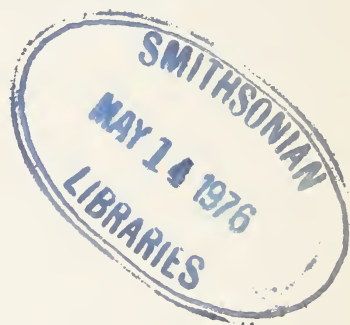
Of the three cobs, one is a segment of connected cupules 15.6 mm long. There are 2.4 cupules per 10 mm of cob length on this and the other two cobs. The broken basal portion has 10 kernel rows and an elliptical cross-section. The kernel rows are even and the butt is unflared. Its median cupule width is 10.1 mm. The tip portion (upper end) has 8 kernel rows and a circular cross-section. The kernel rows are regular and are not strongly paired. Kernel facets are present to the very top of the cob. The median cupule width is 7.8 mm.

Assigning a racial type to this corn can be done only in an evolutionary framework. The low row number (8 and 10 rows), ratio of kernel width to height, and the wide cupules recommend Eastern Complex corn; yet the lack of a flared butt and the broadly separated cupules do not conform with this designation. The reason, of course, is that the classic features of this variety evolved in the east and these samples represent an earlier stage of its development. This corn is not unlike pre-A.D.-1300 maize previously identified from northeastern Arkansas and southeastern Missouri (Cutler and Blake 1973: 9-10, 41).

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THE FIRST AMERICANS: A STUDY OF THE ORIGIN, EVOLUTION AND VARIATION OF THE AMERICAN INDIANS

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ABSTRACT

A well-documented date of entry for the first New World inhabitants has not been established. Evidence shows that man's initial crossing into the New World was by way of the Bering Land Bridge at least 20,000 to 30,000 years ago. Earlier hypotheses attributing biological differences among native Americans to successive waves of migration are not supported by the present findings. There is no evidence that Australoid, Melanesian, Caucasoid or Negroid admixtures have contributed to the formation of the American Indian physical variety. Cultural and/or linguistic similarities between the American Indian and Asiatic Mongoloids have not been fully demonstrated. Studies of living and skeletal morphology have been more useful in reconstructing the past biological affinity of the New World natives. Differences exhibited among modern American Indian groups suggest the possibility that differences in the original Mongoloid stock from which they came have been retained. Since inhabiting the New World, physiological adaptation occurred under a wide range of environmental conditions including subarctic, desert and tropical rain forests, and therefore many of the biological differences can be due to environmental extremes.

INTRODUCTION

The origin and evolutionary history of the American Indians is still a controversial subject argued by archaeologists, prehistorians, geologists, and evolutionary biologists. Despite years of search in the Old and New Worlds for evidence of the origin of the American Indians, a well-documented synthesis of the available information is yet to be offered.

In considering the first New World inhabitants a major problem is the lack of well-dated, comparative osteological material from both Asia and the Americas. When such material is recovered, analysis is limited by several factors. Few

of the reported finds of Paleo-Indian skeletal remains are complete. Often, these finds consist of fragmentary skeletal material that is difficult to reconstruct; so cranial and post-cranial morphology is difficult to determine. Analysis has been further handicapped by the failure of Western scientists to adequately integrate (due to political and linguistic barriers) published data, particularly from Japan and Russia.

It is the intention of this investigation to critically review the available evidence of Paleo-Indian studies and to offer a model by which the present information can be placed into a more useful perspective.

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HISTORICAL REVIEW

Columbus and many of the early Spanish settlers viewed American Indians as less than fully human since they were not mentioned in the Bible. With Las Casa's (1474-1566) appeal, the church gave Indians a human status and agreed that they originated in the Old World. Another widely held theory was that the American Indians were descendants of the "Ten Lost Tribes of Israel." This was first proposed by Amerigo Vespucci after his voyage of 1497. James Adair (Williams, 1930), one of the advocates of this theory, based his hypothesis on phonetics instead of structural similarities between the languages of the two groups. Upon surveying the literature, no biological, linguistic or cultural evidence supporting this theory was found. Jennings, who recently reviewed this theory, concludes,

"Complete lack of tangible evidence—such as the wheel, Old World grains or domestic animals—makes the theory untenable, to say nothing of the common sense problem of how a group of herdsmen and gardeners with no recorded skills of seamanship could have voyaged to the Americas all the way from the dry hills of Asia Minor." (Jennings, 1968: 44-45).

Father José de Acosta in his *Historia Natural y Moral de las Indias*, first published in Seville in 1590, considered the various theories relating to the American Indian origin. While rejecting Atlantis, the Lost Continent of Mu,

and the Ten Lost Tribes of Israel as possible Indian homelands (Beals, 1957; Wilmsen, 1965), he suggested the possibility of a land bridge or a narrow strait in high northern latitudes, over which small groups of hunters crossed to the New World. This appears to be the first time that an Asiatic origin was hypothesized for the American Indian natives. In 1650 Thomas Gage also suggested a Bering Strait route because the American Indians living near the strait were similar to Asiatics in their customs and habits (Thompson, 1958). Meanwhile, European authors were advancing their own hypotheses with regard to the origin of native American Indians. Hugo Grotius suggested Scandinavians, Ethiopians, Chinese and Moluccans as the American Indian's ancestors. Johannes de Laet and George Horn hypothesized that Scythian, pre-Columbian Spaniards, Moduc's Welsh and Polynesians were the forerunners of the American Indians (Winsor, 1889:369-370).

During the 18th century, even more invalid theories for the origin of the American Indians were advanced. Cotton Mather in his *Magnalia Christi Americana* writes,

"Probably the devil decoyed these miserable savages hither, in hope that the gospel of the Lord Jesus Christ would never come here to disturb or destroy his absolute empire over them." (Drake, 1880:24-25).

In 1784 Thomas Jefferson (1801) excavated a small site near his home and recovered a large amount of mastodon bones and teeth. This discovery developed his interest in the American Indians. After further study of Indian languages, he concluded that American Indians and northern Asiatics had a common linguistic origin. Similar conclusions were reached by Father Ignaz Pfefferkorn, S.J. (1794-95) who states,

" . . . in the northern regions America and Asia met or are separated by such a narrow strait that people and animals might pass without difficulty from one continent to the other. To me it is almost certain that the first inhabitants of America really came by way of this strait." (Treutlein, 1949:161).

Lubbock's *Prehistoric Times* was probably the first major work dealing with the history of American Indians. Lubbock (1878) divided their history into four stages: original barbarism, mounds, garden beds, and relapse into partial barbarism. To Lubbock, man's arrival in the New World came as a result of slow population movement, with a few groups entering the New World at any one time. In 1873, Abbott described what may have been a post-Archaic campsite and used it as a basis for explaining the origin of American Indians. After analyzing several hundred artifacts, Abbott suggested an early postglacial date but later (1889:304) concluded, "We are pretty sure of twenty or even thirty thousand years now."

Advocates of the multiple migration hypothesis predominated at the International Congress of Americanists, held at Nancy, France in 1875. Winchell (1880), for example, traced all of mankind from a submerged continent he called Lemuria where he at times even identified the specific tribes who were their descendants. Others gave more valid accounts of the American Indian origin. Dall (1877:93-98) favored a crossing on ice at the Bering Strait and Rau (1822) suggested a land bridge over which man made his crossing to the New World.

After the turn of the century, the fact was established that American Indians did not originate in the New World (Hrdlicka, 1920). For the first time, the question of their origin and evolutionary history was discussed by students with formal anthropological training. New skeletal material was recovered, analyzed and reported. This increased the opportunity for comparative skeletal studies and for communication between researchers interested in American Indian studies. Methods, techniques, and professional treatment and preservation of human skeletal material and artifacts were improved. Systematic site excavations were also employed and more knowledge of past human adaptation became possible. Most important was the rise of anthropological theory with a definite trend toward the integration of various anthropological subdisciplines in Paleo-Indian studies.

During the first half of the twentieth century, polyracialists advanced several theories to explain the origin and physical variability of the New World natives. These theories were based on a typological approach developed in the early days of physical anthropology using cranial measurements and indicial resemblances. Taylor (1946), Gladwin (1947), Howells (1946), Hooton (1947), Imbelloni (1943, 1958) and Rivet (1958) are among such authors.

Taylor (Birdsell, 1951) hypothesized Australoid, Mediterranean and Negroid migrations. Imbelloni (1943) postulated seven distinct human groups entering the New World in the following sequence: Tasmanians, Australians, Melanesians, Proto-Indonesians, Mongoloids, Indonesians and Eskimos. In 1958 Imbelloni revised his earlier hypothesis to include four additional groups. His study was based on stature, robusticity of bone structure, cephalic and head height indices, nasal and facial indices, hair color and form, and skin color. Both skeletal material and observations on living American Indians were used. The eleven varieties were also assigned a chronological order of entry into the New World. Hooton (1947) also attributed physical variability among the New World natives to different migrations. According to Hooton, Eskimos are the most Mongoloid in appearance with a smooth forehead, marked epicanthic eye-folds, a low-rooted and saddled infantile nose and a yellow skin. In North America, and presumably preceding the Eskimo as im-

migrants to the New World, American Indians were characterized by more receding brow ridges, boldly arched noses and coppery skins; in Central and South America are those with wavy hair, very dark skins, and short straight noses. These distributions suggest a series of separate migrations from Asia to the New World, with the earlier waves of immigration being non-Mongoloid (Hooton, 1947).

One of the more controversial arguments to explain the origin of the American Indian natives is that proposed by Birdsell in 1951. Birdsell hypothesized an eastern Asiatic population known as Archaic Caucasoid that was composed of three groups (Murrayians, Carpentarians, and Amurians) during the later part of the Pleistocene. Due to population pressure, Murrayians and Carpenterians were pushed southward where their descendants are today's Australian aborigines. Coon, Garn and Birdsell (1950) suggest that only the eastern branch of the Caucasoids (the Amurians) were represented in northeastern Asia. They further indicate that late in the fourth glacial period in response to stringent environmental conditions, the Mongoloid people evolved from an Archaic Caucasoid stock and spread rapidly. According to Birdsell, the American Indians are hybrids produced by an admixture of Amurian and Mongoloid varieties in which the Mongoloid features became predominant and masked the Caucasoid element. Such admixture, according to Birdsell, is found in groups such as Coahuila tribes of inland southern California and to a certain extent in the Pomo and Yuki of northern California.

Neumann (1952) viewed the differences between American Indian groups as a result of successive migrations. Neumann believes that all but one of his hypothesized eight varieties represent separate migrations to the New World from northeastern Asia. These migrations began with the Otamid variety, a rugged, long-headed people with large mandibles, and continued up to late prehistoric times with the Deneid (Athabaskans) and Inuid (Eskimos) being the latest. Later, however, Neumann (1960) modified his earlier views and offered an evolutionary interpretation to explain the observed physical variability between American Indian groups.

Mourant (1954) and Simmons (1956) suggested that Polynesians and North American Indians could have shared a common gene pool in the not too distant past. Rivet (1958) suggested that the American Indians were the result of four migrations: Mongoloids and Eskimoids (coming through the Bering Strait) and Australoid and Melanesians (coming through the Arctic and Pacific respectively).

W. W. Howells (1946) is not in agreement with the above hypotheses of a non-Mongoloid origin of the American Indians. He argues that the early American Indians were descendants of a generalized Mongoloid stock which

was present during Pleistocene times in northern Asia before the more specialized Mongoloids, such as the Chinese, had developed. Howells further indicates that the groups most similar to the American Indians are those of Indonesia, central Asia and Tibet. Evidence of this generalized American Indian-like Mongoloid variety in Asia is cited by T. D. Stewart (1960) who compared the Late Pleistocene Tzeyang and Liukang crania of western and southern China with American Indian skulls from Florida and California. Stewart also stated that the skulls from the upper cave of Choukoutien (Late Pleistocene) near Peking, China, are similar to those of the American Indians.

Turner (1971), using the incidence of three-rooted mandibular first permanent molars (3RM1), suggested three separate migrations from Asia. The first arrivals were the ancestors of all American Indians except for the Na-Dene (Athabaskans and related groups) who were the second migration. The third group (Proto-Aleut-Eskimo), according to Turner, could have entered the New World at any time during the Upper Paleolithic.

Although linguistic and blood group data support Turner's contention, the use of such data has not been reliable. Swadesh (1960, 1962), on questionable grounds derived from glottochronology, views the majority of American Indian languages to have developed out of the single speech community "Proto-Ancient American." Aleut-Eskimo and Nadenean languages formed a distinctive linguistic group. All North and South American Indians, with the exception of the Athabaskan speakers, show a high incidence of blood group genes O with an extremely low incidence of blood group genes B and A. Athabaskans and related groups show the world's highest known incidence of blood type A. Eskimos and Aleuts are more like Asiatics, particularly in the high incidence of blood type B (Zolatoreva, 1965), with almost equal distributions of blood group genes A, B and O when compared to other American Indian groups. The uncertainty of using blood group gene frequencies in elucidating population affinities and for tracing historical relationships between closely related groups is well-documented (Hanna, 1962; Merbs, 1965). For example, data on the ABO blood systems on Southwestern Indians and Athabaskans (Merbs, 1965) shows Pima Indians to have an incidence more similar to the Ramah Navajo than the latter to other Navajo tribes. Some of the Arizona Apaches of Cibecue and East Fork show distribution more similar to the Pima tribes in Arizona and the Tewan-speaking groups of New Mexico than to the Cedar Creek and San Carlos Apache tribes, also of Arizona.

There are other physical characteristics which clearly distinguish the American Indians from Aleuts and Eskimos. According to Laughlin (1967), Eskimos and Aleuts, along with the Chuckchi, Koryak, and possibly the Kamchadal encircle the Bering Sea and compose a biologically related group, the Bering Sea

Mongoloid. In their physical characteristics, Eskimos and Aleuts (Laughlin, 1950, 1963, 1966, 1967) have many common elements that establish a close affinity with the Chuckchi and Asiatic Mongoloids, rather than with American Indians. Common features are large heads and faces, large mandibles, high frequency of mandibular torii, thickening of the tympanic plate which is often pronounced, and narrow nasal bones often achieving a world extreme in Eastern Eskimos. There are many dental traits common to Eskimos and Aleuts, but not American Indians. Among these are the frequent absence of third molars, the large lateral as well as medial incisors, and the three-rooted mandibular first permanent molars. Physiologically, the Eskimos display differences from Indians in their cold adaptations, especially in their elevated basal metabolism (Milan, 1963). Eskimos also have a high incidence of separate neural arches and other anomalies, again showing a greater affinity with Asiatic Mongoloids than with the American Indians (Merbs, 1963).

THE BERING STRAIT

It is now accepted that man's first crossing from Asia into the New World was by way of the Bering Land Bridge connecting Siberia and Alaska some time during the Late Pleistocene (Hopkins, 1967). Who were these people? How did they get here?

Where the Bering Strait now exists, a broad land area called Beringia (western Alaska, northeastern Siberia and the shallow parts of the Bering Sea and Chuckchi Sea) was present several times during the Wisconsin glacial stage (Butzer, 1971). The Bering Strait is only 56 miles wide at its narrowest point. A land bridge would form if sea level dropped 120 feet below its present level (Solecki, 1951a, 1951b; Creager and McManus, 1967) connecting Siberia and Alaska by way of St. Lawrence Island (Fig. 1).

Geological evidence shows that the Wisconsin glacier reached its maximum about 40,000 years ago and lowered the sea level by about 460 feet (Haag, 1962). The bridge was submerged again approximately 28,000 to 25,000 years ago. On the basis of climatic evidence, the land bridge could have lasted from about 25,000 to about 11,000 years ago. The lowering of the sea level exposed nearly all the Bering-Chuckchi platform connecting Alaska and Siberia by a plain extending from the north shore of the shrunken Bering Sea to the south shore of the Arctic Ocean (Hopkins, 1959). According to Chard (1959), northeastern Asia and Alaska were glaciated only in the mountainous regions even during the maximum extension of the ice sheets. The coastal plains of northeastern Alaska were free of ice and much easier to travel than the mountainous region to the south. Furthermore, neither the Chuckchi Peninsula in Siberia nor the Seward

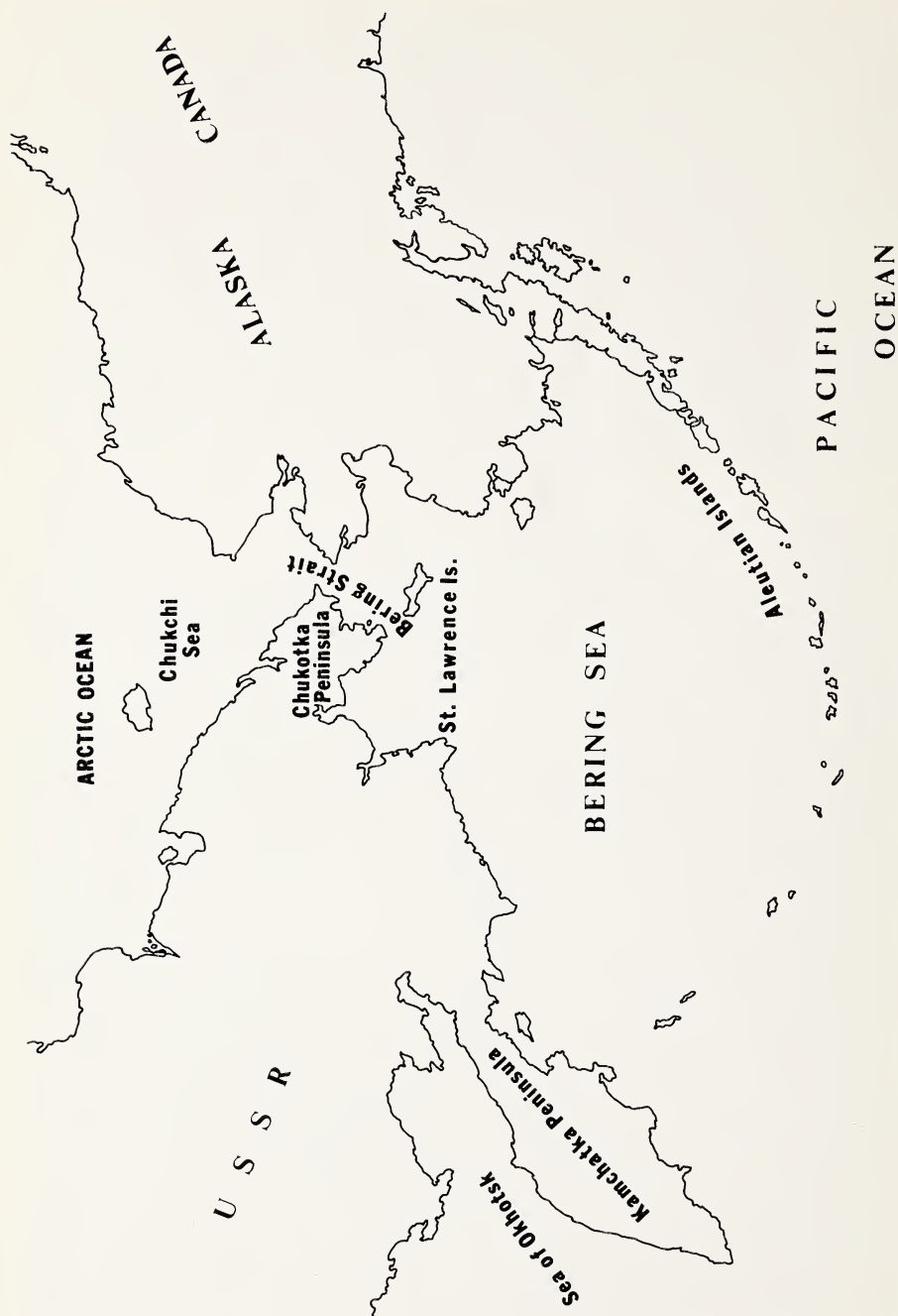


Figure 1.

Peninsula of Alaska were glaciated during the Wisconsin period. The Bering Land Bridge which also existed at the same time was glacier-free, making the crossing even easier. With no physiographic barrier, Asiatic people and animals could have moved freely across the land bridge during most of the Wisconsin Stage. Haag (1962) indicates that fossil evidence for the origin and geographic distribution of North American mammals shows that many animals crossed the Bering Land Bridge to the New World during the Wisconsin Stage. These include mastodon, mammoth, musk oxen, moose, bear, bison, mountain sheep, goats, elk, camels, fox, wolves and horses (Haag, 1962:114).

During the Late Pleistocene the environmental conditions of Beringia were very similar to those of northeastern Siberia (Colinvaux, 1964). The abundance of horse, bison, woolly mammoth, antelope and yak made this area economically attractive to the Asiatic hunters. Following the game, these hunters moved eastward until this pursuit led them unknowingly across the Bering Land Bridge into Alaska and on to North and South America. These migrants may have moved into the New World on the winter pack ice even when the land bridge was submerged. It is also possible these first Americans had developed small sea crafts capable of negotiating the Bering Strait.

It is conceivable that Asiatic hunters deliberately undertook a long journey into an unknown land. Population movement appears to have been sporadic and to have spread slowly. Population pressure, abundance of game and climatic conditions were both motivating and limiting factors which determined the magnitude and rate at which the first migrants moved out of Asia. Those who made the crossing were probably adapted to the conditions of the peri-glacial ecosystem, and had developed adequate tools and hunting techniques. These people spread eastward along the Alaskan foothill country, then southward. The advantages of traveling such a route have been outlined by Irving (1953). These areas (1) are comparatively dry in contrast with the wet lowland tundras, (2) are good for sighting game, (3) offer the advantage of both forest and tundra, being open enough for pursuit of game but with enough tree and bush cover to provide shelter, (4) are preferred routes for major game trails that are otherwise restricted by rugged mountains and soggy grounds. Wilmsen (1965) suggests it is important to note that this was the only type of environment which might be virtually continuous from central Siberia to central North America during glacial periods. Once on Beringia, with the advantages of sea, rivers and nearby forests, some of these human bands may have become established with permanent occupations. As the Bering Sea Platform slowly submerged due to warmer temperatures, some group dispersal to the interior may have occurred. These hunters would not have the tendency to go back to Siberia but rather to push forward toward the interior.

EVIDENCE FROM THE NEW WORLD

The oldest carbon 14 dated New World human skeleton (skull) is Los Angeles Man at 23,600 B.P. (Wormington, 1971), and the Laguna Beach skull dated at about 17,000 B.P. (Berger and Libby, 1969). The best dated skeletal remains are the $10,750 \pm 500$ B.P.-year-old cranium fragments from Marmes, Washington.

In North America, Indian cultural traditions are usually subdivided into three successive though overlapping horizons on the basis of their style: Llano, Folsom and Plano. The Llano complex, including Clovis and Sandia points, dates some time around 10,000 to 12,000 years ago. The Llano is an early plains hunting complex known mainly from sites in the southwestern United States and Mexico, of which Lehner Ranch (Haury *et al*, 1959) and Blackwater Draw (Sellards, 1952) are typical. Clovis points have been dated at 9250 ± 300 B.P. at the Naco Site in Arizona, and seven other radiocarbon dates at Lehner Site range from 7022 ± 450 to $12,000 \pm 450$ B.P. (Haury *et al*, 1959). Folsom points seem to have been the regional development of the Llano. A shift from mammoth to bison hunting is evident between the Llano and Folsom Sites, but there seem to be no major structural changes between the artifact assemblages (Willey, 1966). Folsom points have been dated at three places. The Lubbock Site in the Texas Panhandle is dated at 9883 ± 350 B.P. (Sellards, 1952), the Lindenmeier in Colorado at $10,780 \pm 375$ (Haynes and Agogino, 1960), and Brewster in eastern Wyoming at $10,375 \pm 700$ (Krieger, 1964). At Graham Cave, Missouri, and Modoc Rock Shelter in Illinois, points of "plano" types range from 8830 ± 500 to $10,651 \pm 651$ B.P. A date of $11,200 \pm 800$ comes from the bottom of the Modoc Rock Shelter (Krieger, 1964).

There is other evidence suggesting that man's arrival in the New World could have occurred much earlier. The evidence for such an early appearance comes from several sites in North and South America, and is based on artifact assemblages. In general, these "hypothesized" tools are crude, percussion-flaked tools, scrapers, and choppers. Most of these claims for the "pre-projectile point" cultural tradition rests on typology alone.

The earliest of the radiocarbon dates for these suggested tools in the New World come from Lewisville, in northern Texas. Twenty-one hearths, fossil bones, charred hackberry seeds and a crude chopper or scraper show some evidence of human occupation (Crook and Harris, 1957). A date of 37,000 B.P. has been determined. The antiquity of this site has been challenged and the hearths are not believed to have been man-made (Heizer and Brooks, 1965). The clovis-type projectile points recovered suggest either a mixture of later material with earlier geological strata or the points were simply "planted"

there. On Santa Rosa Island dwarf mammoth bones and burned bone fragments gave a radiocarbon date ranging from 30,000 to more than 37,000 years ago. Only one specimen of what possibly is a crude chipped-stone has been found with any of the hearths or bone deposits (Orr, 1968). Radiocarbon dates on "presumed" charcoal from Tule Spring in southern Nevada were more than 23,000 and 28,000 years old (Harrington and Simpson, 1961). Recent excavations at Tule Springs do not lend support to the original claims. Laboratory analysis has shown that the dark, carbonaceous materials from the supposed "hearths" may not have been entirely charcoal. The earliest evidence of man's presence at Tule Springs is now placed at about B.C. 11,000 (Bryan, 1964; Shutler, 1965).

The earliest definite proof of man's presence in South America comes from two localities: the Chivateros I complex in the Chillon Valley of the central coast of Peru and Lagoa Santa, Brazil. Radiocarbon dates have placed the end of the Chivateros I occupation at B.C. 8500 (Willey, 1966). At the Lagoa Santa caves and rock shelter, fauna, artifacts and human remains were recovered. Those from levels 2 and 3 averaged 9311 ± 120 B.P. and levels 6 and 7 averaged $10,024 \pm 127$ B.P. (Hurt, 1962). Cruxent (1968) has proposed an arrival date in South America of 15,000 to 20,000 years ago. This hypothesis was based on the following finds: El Jobo, 10,000 years; Las Lagunas and El Camare, more than 16,000 years; and Muaco, 14,740 to 16,580 years (Rouse and Cruxent, 1962). Lanning and Patterson (1967), estimated the Chuqui complex in Chile and the Tortuga and Red Zone complexes in Peru as the most ancient in the Pacific Andean region, both dating between 13,000 and 14,000 B.P. Other rough stone tool complexes from South America which have been suggested as belonging to a pre-projectile point horizon include: Viscachani in Bolivia (Krieger, 1964); Ghatchi I in northern Chile (La Paige, 1958, 1960; Krieger, 1964); Ampajango in northwestern Argentina (Cigliano, 1961); Tandilense in Argentine Pampas (Menghin and Bormida, 1950); Oliense in Argentine Patagonia (Menghin, 1952) and early Rio Chico, Tierra del Fuego (Viganti, 1927). An excellent survey of early man in the New World is given by Wormington (1971).

EVIDENCE FROM ASIA

Several lines of evidence (Stewart, 1960) show that during the middle Late Pleistocene, early forms of primitive Mongoloids were present in northeastern Asia. Many of these have been implicated in the origin and evolution of recent Mongoloids and Mongoloid-affiliated human groups. The most primitive, con-

sisting only of a skull cap, was found in 1958 in a limestone cave near the village of Mapa in Kwangtung province in southern China. According to Woo and Peng (Coon, 1962) this is the earliest fossil so far found in China with the exception of the *Homo erectus* material from Choukoutien. Woo believes that the Mapa skull had evolved to the same grade as the European Classic Neanderthals. According to Coon (1962) the Mapa skull stands at the threshold between the two grades of *Homo* and that it is essentially Mongoloid in its morphology. The second find (Liukiang man) was discovered in a cave near Liuchow in the Kwangsi Chuang Autonomous region, also in southern China. According to Woo (Coon, 1962), the Liukiang man represents an early form of the evolving Mongoloid and is the earliest fossil representative of modern mankind so far found in China. The third (Tze-Yang) was found in 1951 in the Szechuan province about 700 to 800 miles southwest of Peking. Woo described the Tze-Yang find as an early form of *Homo sapiens* more primitive than the European Cro-Magnon and the upper cave people of Choukoutien. According to Coon (1962) the Tze-Yang skull falls within the female range of both Metal Age Prehistoric and recent North Chinese series and is essentially a *Homo sapiens*.

There are no archaeological sites in Siberia having carbon 14 dates in excess of 25,000 years (Skimkin, 1968). According to Debetz (1960) all early Siberian sites are of the Upper Paleolithic tradition and are concentrated in the Lake Baikal region. Neanderthal-Mousterian sites have not been found so far in Siberia, even though Mousterian culture remains are the best established ancient occupation in Russia, along the Volga River and in Turkestan (Debetz, 1960).

The earliest Paleolithic sites in eastern Siberia are located around the Lake Baikal region. The oldest of these sites date around B.C. 20,000 (Bushnell and McBurney, 1959). Of the Paleolithic sites, the best known are those reported from the Lake Baikal region including Malta (14,750 B.P., Butzer, 1971) and Buret. Artifacts include points, sidescrapers, knives, burins, semi-subterranean structures employing mammoth bones, a variety of venus figurines and bone needles. Two sites are of particular interest: Duiktai cave with a single date of 13,070 B.P. including bifacial, pressure-flaked projectile points and knives in association with a mammoth fauna, and Uski with a date of 14,300 and 13,600 for levels VI and V with bifacial foliate points and knives.

Other finds in China, particularly those from the Upper Cave of Choukoutien, are of great interest. These remains provide the only information of the terminal Pleistocene population of eastern Asia from which the New World natives most likely came.

The two female skulls were described by Weidenreich (Coon, 1962) as a

Melanesian (102) and an Eskimo (103). This conclusion was based on a preliminary interpretation of the unrestored skulls. His assumption that the male skull (101) is an Ainu has also been questioned. Weidenreich made his comparison on the basis of photographs sent him by S. Kodanei (Coon, 1962) who at the time was working on Ainu craniology in Japan. Comparing skull number 101 with those from a series of Ainu skulls from Hokkaido, Sakhalin and the Kuriles, Coon reports many significant differences. For example, the cranial length of the Upper Cave skull is 16 mm greater than the largest Ainu mean. The minimum breadth of the Upper Cave skull is 11 mm greater and the nasal height is 5 mm higher than any Ainu average, and bi-orbital diameter is 9 mm beyond any Ainu mean. According to Coon (1962), the Upper Cave skull resembles the large-faced tribes of the American Plains Indians. Coon concludes that this is particularly visible in the upper part of the nasal skeleton and the lateral borders of the orbits, but the molars and the lower part of the nasal skeleton are fully Mongoloid in the eastern Asiatic sense. Morphological traits of the Upper Cave skull also appear commonly in various American Indians and the differences may simply reflect the range of variability of these groups. Indeed, these skulls have been referred to by W. W. Howells as "Unmigrated American Indians" (Howells, 1940).

DISCUSSION

The Asiatic origin of the New World natives is now a generally accepted fact. There are few serious students who any longer question either the general genetic or geographic origin of the first human inhabitants of the Americas or the basic routes of their initial entry. All remains recovered thus far in the New World are *Homo sapiens*.

Culturally, linguistically and genetically, American Indians are more closely related to Asiatics than to any other human group. Earlier hypotheses attributing biological differences between American Indian groups to waves of migrations from diverse parts of the Old World are not supported by the present findings. There is no evidence of any element other than Mongoloid in the formation of the American Indian physical variety. All evidence points to an Asiatic homeland for the New World natives.

There is no valid evidence that Australoid, Caucasoid, Negroid and Melanesian migration to and/or admixture in the New World contributed to the American Indian physical variety. For example, if the American Indians are derived from a Mongoloid-Australoid admixture then they should have blood group N which is very common among Australoids. Actually the American In-

dians have one of the lowest incidences of N in the world. Moreover, Australoids have facial and body hair, large teeth (often exceeding those of classic Neanderthal) and they lack the wide, flat faces, heavy noses, and pronounced cheek bones characteristic of the American Indians. The Australoid skin color and hair form are also very different from those of the American Indians. If Negroid genes were present in the American Indians then R_o , the sickle cell and thalassemia genes, the African form of G6PDD, the rare gene V and the Duffy variant, as well as other hemoglobin polymorphisms should be present. None of the above blood characteristics are found in the American Indian. Moreover, skull form characteristics also differentiate American Indians from Negroids.

If Caucasian genes are present, the Rh-negative and blood group type A should be common. These genes are nonexistent in the American Indians with the exception of Athabaskans and related groups who have a high incidence of blood type A. Caucasoid features not found in the American Indian are small teeth, high incidence of Carabelli's cusp, delayed tooth eruption, skin and hair color, sickle cell and thalassemia genes, G6PDD and familial Mediterranean fever. Melanesians differ in physical characteristics from American Indians by having darker skin, and hair that curls, twists and frizzes. There is a higher incidence of G6PDD, blood groups B and N. Melanesians possess the thalassemia gene and are subject to constant selection by a vast number of virulent diseases (Garn, 1972).

On the other hand, the evidence strongly indicates that eastern Asiatics are the most closely related to the American Indians. The straight, dark hair, wide, flat faces, heavy noses, the tendency toward a Mongoloid eye, scant body hair, and the prominence of the cheek bones are characteristics of eastern Asiatics which are always present among American Indian natives.

That today's American Indians differ from living Asiatics in the incidence of certain blood group genes can be explained as follows. First, American Indians crossed the Bering Land Bridge at the time when genetic differentiation in the original Mongoloid stock was taking place, and thus original differences within this stock have been retained. Second, a number of migrations did take place at different times and from separate areas, but still from groups falling within the range of variation of the generalized Mongoloid stock. Third, since the peopling of the New World, American Indians have been evolving on their own, and differences between them and their Asiatic relatives can be attributed to genetic drift and natural selection operating under variable environmental conditions. Fourth, it is only in the simply inherited blood group genes that the differences are most apparent. Multifactorial (polygenic) traits, e.g. hair form, color, facial characteristics, shovel-shaped teeth, etc., do not

show such differences to exist among American Indian groups or between them and their Asiatic relatives.

Viewed as a geographic entity and a physical variety of its own, American Indians consistently show extreme values of several traits such as high shovel-shaped teeth, low Carabelli's cusp, the world's highest incidence of blood group O, Rh-positive gene, high incidence of blood group M, the secretor gene, the Diego positive gene (Di^a) which set them apart from other major geographic groups and suggest basic genetic similarities producing a unique constellation of physical characteristics. T. D. Stewart (1960:262) states, "Indeed, it is safe to say that no population of comparable size has remained so uniform after expanding in whatever time has been involved, over such a large area."

There are no clear-cut cultural or linguistic similarities between American Indians and Asiatics. Boas (1940) indicates some similarity of the absolute pitch of South American and eastern Asiatics' musical instruments, the use of birch bark for making vessels, canoes and for building houses, and the use of slat armor and flat drums. Similarities in religious ceremonials, beliefs and traditions have also been suggested by Boas (1940). Recently, Chard (1960) suggested an apparent late "North Pacific Continuum" from Kamchatka to Puget Sound.

Wilmsen (1964) has considered the possible cultural relationships between the Old and New Worlds. He proposed a cultural-ecological continuum and a technological relationship that extends from Siberia all the way into the interior of North America. Two New World archaeological assemblages were considered as follows (see also MacNeish, 1959): the Kogruk Complex from Anaktuvuk Pass in north-central Alaska, and the British Mountain Complex from the fifth River Delta on the Arctic Coast of Yukon Territory, Canada. Between Siberian and British Mountain materials MacNeish (1959:46) states,

"The earliest occurrences of these resemblances is the Buryet (Buret)-Malta complex of the Trans-Baikal and perhaps it also occurs at the Chastino site of the Middle Lena. Here are also found tools struck from discoidal cores that include unifacial points both lenticular and lanceolate, hooked graters, scrapers and central convex-type burins . . . end of blade scrapers and blades and pebble choppers."

According to Campbell (1961:16-17):

" . . . Kogruk implements somewhat resemble points, perforators, scrapers and blades from the earliest levels of the Malta site . . . Siberian Paleolithic sites in the Lena River Valley have produced artifacts quite closely akin to Kogruk flakecores and blades . . . There are, apparently, even closer connections between the British Mountain complex and these Asian collections, especially in the categories of flake burins and bifaces."

Since little information of the skeletal biology of the Mongoloid stock from which American Indians originated is available, most archaeologists find themselves highly dependent on lithic material for questions of origin. There are certain important limitations in using lithic material for evidence of tracing and reconstructing past biological relationships. Skeletal and genetic data are more useful.

Cultural similarities can be indicative of biological affinity. This relationship is not always valid. Similar cultural developments are known to exist in several parts of the world without any evidence of biological resemblance. Archaeologists must recognize that several thousand years may have elapsed before Asiatic migrants reached the New World. New tools and techniques could have developed en route. Tolstoy (1958) has made an extensive study of Old and New World relationships and has concluded that many Paleo-Indian traits, especially parallel-flaking and fluting, were of New World origin.

Chard (1959a, 1959b) suggests that the only Siberian and far eastern Asiatic Paleolithic cultures that were clearly old enough to have provided the cultural heritage for the early immigrants were the chopping tool industries characterized by rough core tools, choppers and scrapers but lacking both bifacial blades and points. It was this kind of technology, according to Chard, that was carried to the New World, and it was in the Americas over a span of several thousand years that the distinctive bifaced, lanceolate projectile point types evolved independently of any further Asiatic influence. As Wormington (1962) has suggested, archaeologists should not look for duplications of New and Old World tools but rather for prototypes from which New World tools were derived. After all, the American continent was essentially isolated from the Old World for several thousand years. This was time enough for Paleo-Indians to develop a diverse variety of tools which were compatible with the changing environmental conditions ranging from subarctic to high mountains and low deserts.

At present, no evidence of a relationship between the American Indian and Old World languages has been demonstrated (Willey, 1966). Indian-Asiatic linguistic affinity is very distant, if it exists at all. The fundamental structural differences in Siberian languages make it difficult to trace the origin of the American Indian languages. In North America alone, at least six major linguistic stocks are known to exist. The total separate and mutually unintelligible languages exceed 200 (Jennings, 1968:4). The influx of the Tungus and Turkish tribes into Siberia, although recent, also disturbed the earlier distribution in one way or another, making the tracing of such relationships impossible (many aboriginal languages in Siberia are no longer spoken). Shafer's (1952) hypothesis that the Athabaskan language is related to Sino-Tibetan is

only weakly supported. Kiparsky's (1968) suggestion that there was contact between Sahaptian and Chuckchi-Kamchada speakers is also weak, resting on the shared trait of diagonal vowel harmony. Thus it appears that until more information is available any statement concerning linguistic affinity can be no more than speculative.

At this point it is important to recognize that Asiatic Mongoloids and those who migrated to the New World have been independently evolving culturally, linguistically, and biologically since their geographic separation. Individual American Indian groups were generally small and isolated, particularly during pre-Columbian times, thus maximizing the chance for genetic diversity between these groups and decreasing variability within such groups. The picture of only a few small groups actually completing the crossing into the New World is compatible both with geological and environmental conditions and with the observed degree of biological differences among the New World natives. The high frequency of blood group gene O and virtual absence of B and A in North and South America with the exception of Athabaskan speakers and the presence of A, B and O in Eskimos and Aleuts could suggest that early differences have been retained. A more plausible hypothesis is that the simply inherited blood group genes change at a much faster rate than the multifactorial (polygenic) traits, which show similar incidence among all New World natives. Other characteristics of certain American Indian natives, such as large chest, lungs and hearts among Andean groups in South America are primary adaptive responses to the environment. The prominent nose and projecting chin of the Plains Indians, the high frequency of dislocated hip among the Navajos and Apaches, the beard hair among the Paiute and the Coahuila, the albinism among Hopi, Zuni, Jemez and San Blas, and the obesity among Pima and Papago are traits either environmentally determined or were brought about by the action of selection, genetic drift and other genetic determinants acting on small isolated groups.

At present, virtually nothing is known about the rate of evolution among human populations. Genetic differences often observed among prehistoric and recent historic skeletal and/or living American Indian groups can be explained without invoking hybridization and/or multiple migrations. Genetic drift and/or natural selection may have operated singly or in combination to produce the observed differences. The first New World inhabitants arrived during the phase of evolution in which differentiation in the original Asiatic stock was taking place. Since then, physiological adaptations occurred under an extreme range of environmental conditions including subarctic, desert, and tropical rain forests, and therefore, biological differences can simply be attributed to environmental extremes. Under such conditions, genetic varia-

tion, without obscuring the basic assumption of the genetic homogeneity of the American Indians, is expected. Reconstruction of the general Mongoloid physical type, as well as environmental conditions which existed at the same time as the hypothesized migrations, is crucial and must be thoroughly investigated. There is a further need for the recovery of skeletal and cultural materials from submerged sites on the continental shelf, which would shed more light on the nature of migration(s) into the New World.

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A NEW CRINOID FROM THE PUTNAM HILL LIMESTONE MEMBER (ALLEGHENY GROUP, PENNSYLVANIAN) OF OHIO

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ABSTRACT

An inadunate crinoid, *Diphuicrinus ohioensis* sp. nov., from the Putnam Hill Limestone, Allegheny Group, Middle Pennsylvanian of Ohio is described. Features of the dorsal cup that characterize the species are (1) width more than three times the height, (2) similarity to cups of *D. patina* Strimple and Knapp and *D. coalensis* Strimple and Moore in lateral profile, (3) pentagonal outline in ventral view, (4) radial forefacets less deep than internal facet areas, (5) prominence of anal X, and (6) small nodes on infrabasals and proximal portions of basals; large discrete nodes on remainder of cup.

The genus *Diphuicrinus* Moore and Plummer, 1938, is considered to compose an aberrant line of Pennsylvanian crinoids and to be the sole representative of the family Diphuicrinidae. The genus *Graffhamicrinus* Strimple, 1961, is regarded as invalid, because based on surface ornament, an inadequate criterion for generic distinction; the genus is here treated as a junior subjective synonym of *Delocrinus* Miller and Gurley, 1890. Study of the holotype of *Delocrinus aristatus* Strimple shows it to be a typical representative of *Diphuicrinus*; the species is here designated *Diphuicrinus aristatus* (Strimple, 1949) comb. nov.

INTRODUCTION

Specimens comprising the types of a new species of the Pennsylvanian crinoid genus *Diphuicrinus* described in the following pages are repositied in the Cleveland Museum of Natural History (CMNH), the National Museum of Natural History (USNM) and Orton Museum, Ohio State University (OSU). The Orton Museum specimens were formerly in the collection of the Geology Depart-

ment of Ohio University. Dr. Myron Sturgeon of that institution kindly permitted me to describe them.

I am indebted to Dr. Patrick Sutherland of the University of Oklahoma (OU), to Mr. Harrel Strimple of the University of Iowa (SUI), and to Mr. James Murphy of Case Western Reserve University for the opportunity to study crinoid material pertinent to this investigation. I thank Dr. Mildred Walmsley for technical assistance in preparation of this paper.

REGISTER OF LOCALITIES

All of the crinoid specimens designated as types of the new species described herein were collected from shaly portions of the Putnam Hill Limestone Member, Allegheny Group, Pennsylvanian, in Elk Township, Vinton County, Ohio, near the town of McArthur. Morningstar (1922) applied the name McArthur Limestone to the unit from which these crinoids were taken, but the name Putnam Hill Limestone (Andrews, 1870) has priority over Morningstar's appellation and is the term currently used in Ohio. Locations of the collecting sites are given in the following summary:

Locality 1: Abandoned strip mine east of township road 17, in the SE $\frac{1}{4}$ sec. 7, Elk Twp., Vinton County, Ohio (lat $39^{\circ}16'45''$ N., long $82^{\circ}30'31''$ W.) 4.4 km northwest of McArthur, Ohio.

Locality 2: Abandoned strip mine NE of township road 17, in the NE $\frac{1}{4}$ sec. 17, Elk Twp., Vinton County, Ohio (lat $39^{\circ}16'26''$ N., long $82^{\circ}30'10''$ W.) 3.5 km northwest of McArthur, Ohio.

Locality 3: Abandoned strip mine in the NE $\frac{1}{4}$ sec. 17, Elk Twp., Vinton County, Ohio (lat $39^{\circ}16'35''$ N., long $82^{\circ}29'40''$ W.) north and east of a tributary of Elk Fork, and 3.4 km northwest of McArthur, Ohio. The original label notes that the locality is "across the ravine from the old Moore mine." The Moore mine was designated the type locality of the McArthur Limestone by Morningstar (1922).

SYSTEMATIC PALEONTOLOGY

Class CRINOIDEA Miller, 1821

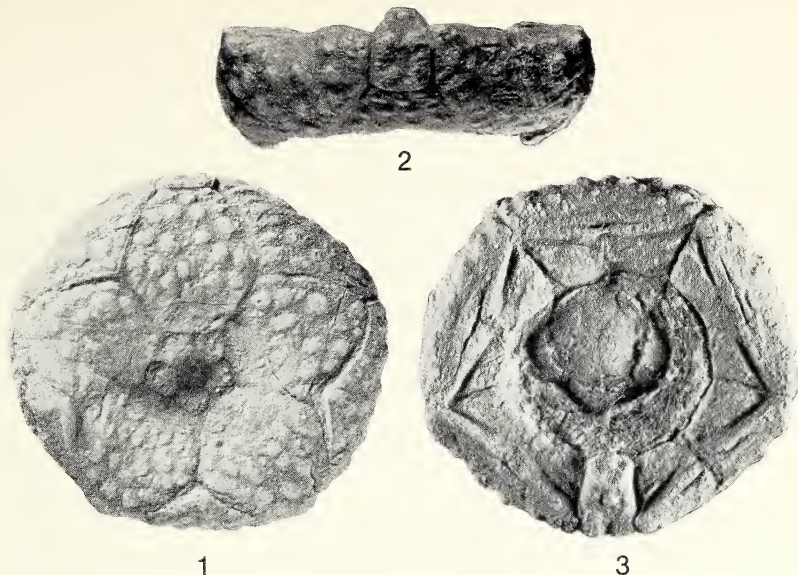
Family DIPHUICRINIDAE Strimple and Knapp, 1966

Genus DIPHUICRINUS Moore and Plummer, 1938

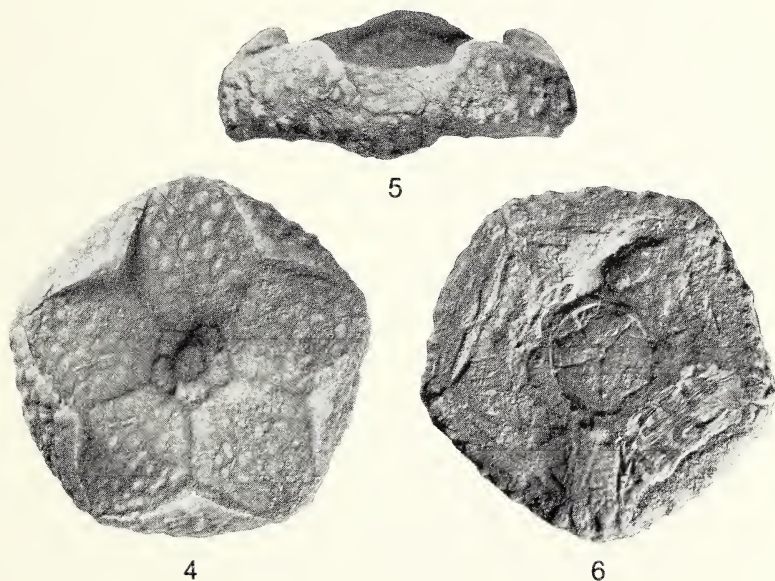
Diphuicrinus ohioensis sp. nov.

Figs. 1-9

Diagnosis: Dorsal cup more than three times wider than high (H/W ratio about 0.30) and near that of *D. coalensis* Strimple and Moore in size; resembles cups of *D. coalensis* Strimple and Moore and *D. patina* Strimple and Knapp in lateral profile; outline somewhat rounded in dorsal view, pentagonal in ven-



Figures 1-3. *Diphuicrinus ohioensis*, sp. nov. Holotype, CMNH 3800, from the Putnam Hill Limestone, Allegheny Group, Vinton County, Ohio. Fig. 1, dorsal view; fig. 2; posterior view; fig. 3, ventral view. All x2.



Figures 4-6. *Diphuicrinus ohioensis*, sp. nov. Paratype, OSU 31504, from the Putnam Hill Limestone, Allegheny Group, Vinton County, Ohio. Fig. 4, dorsal view; fig. 5, posterior view (dorsal side up). Note collapsed basals, and radials still in place. Fig. 6, ventral view. All x2.

tral view; radial forefacet less deep than internal facetal area; anal X a prominent component of cup. Principal ornament large discrete nodes on anal X, radials and distal portions of basals; smaller nodes on infrabasals and proximal region of basals.

Types: Holotype CMNH 3800, collected by Delbert Windle. Paratypes: OSU 31504, collected by Myron Sturgeon and Richard Hoare; OSU 31503, collected by Don Crissinger; USNM 166575 and USNM 166576 (partial dorsal cup), both collected by James Murphy.

Occurrence: Putnam Hill Limestone Member, Allegheny Group, Pennsylvanian.

Localities: Elk Township, Vinton County, Ohio (see Register of Localities). Holotype, CMNH 3800 and paratype OSU 31503 from Locality 1. Paratype OSU 31504 from Locality 2. Paratypes USNM 166575 and USNM 166576 from Locality 3.

Description: Dorsal cup low truncate bowl-shaped, more than three times wider than high, rounded pentagonal in dorsal outline, pentagonal in ventral. Lateral walls steep. Height and width dimensions of basal impression more than half those of the cup. Slopes of impression moderate. Infrabasals convex, discrete, gently downflaring, of medium size.

Basals with moderate but steepest slopes within basal impression; nearly flat proximally, maximum longitudinal curvature in vicinity of basal plane, less along lateral wall; slightly concave transversely in region of basal plane. Interbasal sutures inconspicuous. Distal borders of basals slightly curved. Except for CD basal, little exposure of basals on lateral wall. CD basal quite elongate, truncate distally.

Proximal tips of radials mark basal plane. Radial slopes gentle proximally, conforming with those of basals, but steep along lateral wall. Transverse convexity of radials slight. Forefacet less deep than internal facetal area. Outer facetal ridge sturdy in holotype. External ligament pit slitlike, transverse ridge elevated, remarkably slender and sharp, denticulate. Inner facetal area faces inward. Lateral furrows narrow. Adsutural slopes steep, adsutural valley floors rising with lateral ridges. Lateral lobes with winglike borders. Intermuscular notch very broad. Intermuscular furrow short, extends to intermuscular elevation separating rounded muscular-basin areas.

Anal X slightly damaged in holotype, partly recumbent and moderately elevated on internal side, with about one-third of height above summits of radials; shows two distal facets; proximally rests on truncated tip of CD basal. In all the types anal X is prominent component of cup.

Ornament of basals, radials and anal X consists mainly of fairly large, well-separated nodes, with a few small nodes scattered among them. Small nodes

predominant on proximal parts of basals. Small nodes also present on infra-basals.

Measurements: Linear measurements, in mm, taken on two specimens are as follows: CMNH 3800 (holotype) - Dorsal cup height, 7.1 (appr.), width, 24.0 (appr.), H/W ratio, 0.30, basal impression height, 4.0, width, 13.0; infrabasal circlet, width, 5.7; basal (EA) length, 8.4, width, 8.7; radial (A) length, 6.7 width, 12.8; suture between basals, length, 4.7 (appr.), suture between radials, length, 4.0; anal X, height, 5.9, width 3.9. OSU 31504 (paratype) - Dorsal cup height, 7.1, width 22.2, H/W ratio, 0.32; basal impression width, 13.8; radial (E) length, 6.6, width, 12.6.

Comparisons: Dorsal cups of *Diphuicrinus ohioensis* sp. nov., *D. patina* Strimble and Knapp, and *D. coalensis* Strimble and Moore agree in showing, in lateral profile, subparallel, almost plane, dorsal and ventral borders, steep lateral walls (least steep in *D. coalensis*) and width of cup more than three times the height. In dorsal and ventral views, *D. patina* is more rounded; in ventral view, *D. ohioensis* and *D. coalensis* are definitely pentagonal. In *D. patina* the radial forefacet is as deep as the internal ligament area; in *D. coalensis* and *D. ohioensis* it is less. In *D. ohioensis* the large nodes are more prominent; they are also more discrete than in *D. patina*, less sparse than in *D. coalensis*. The infra-basals are nodose in *D. ohioensis*, not ornamented in *D. patina*, and evidently not ornamented in *D. coalensis* also. Anal X is a prominent plate in *D. ohioensis*, of moderate size in *D. patina*, and reduced in *D. coalensis*. The holotype of *D. ohioensis* greatly exceeds that of *D. patina* in size, but is nearly the same size as the holotype of *D. coalensis*. The figured paratype of *D. patina*, SUI 11901 (Strimble and Knapp, 1966, fig. 23) which is larger than the holotype of *D. patina*, quite clearly does not belong to that species, and possibly does not pertain to *Diphuicrinus*. It shows peculiar depressions along the interbasal sutures that are not characteristic of *Diphuicrinus*, but the dorsal cup is too poorly preserved for definite allocation.

Discussion: Moore and Plummer (1937, p. 311) indicated that they based the genus *Diphuicrinus* on "the structure of the calyx, including the deep ligament fossae of the suture faces . . .". The deep ligament fossae are a characteristic feature of *Diphuicrinus*, it is true, as shown both by isolated plates and by plates still in association within the cup. However, the fossae do not persist throughout the life span of the animal. Some isolated radial and basal plates display them on all suture faces. These plates must pertain to young animals, for other plates show the fossae filled with calcareous upgrowths that make flush contacts with similar deposits on suture faces of adjoining plates. Along such contacts the plates tend to be bound together; apparently at this stage they were connected, not only by ligaments, but also by calcareous deposits. This last stage is first

traceable along the interr radial sutures (and along the sutures between the posterior radials and anal X). It is not unusual to find specimens of *Diphuicrinus* in which the basals, although still lying within the dorsal cup, have fallen away from sutural contact with the radials and infrabasals. My paratypes of *Diphuicrinus ohioensis* demonstrate this (see Figures 4-5). The radials of these dorsal cups continue to remain upright, bound together interr radially in normal position in the cup. At later growth stages, however, the other fossae of the radials and those of the basals became filled with calcareous deposits also, and if the cup is preserved the plates are usually found in place, as they were in the living animal. This seems to hold for the three dorsal cups included in the type suite of *Diphuicrinus croneisi* Moore and Plummer, the type species of the genus, and may be taken as indicating a degree of maturity for these specimens.

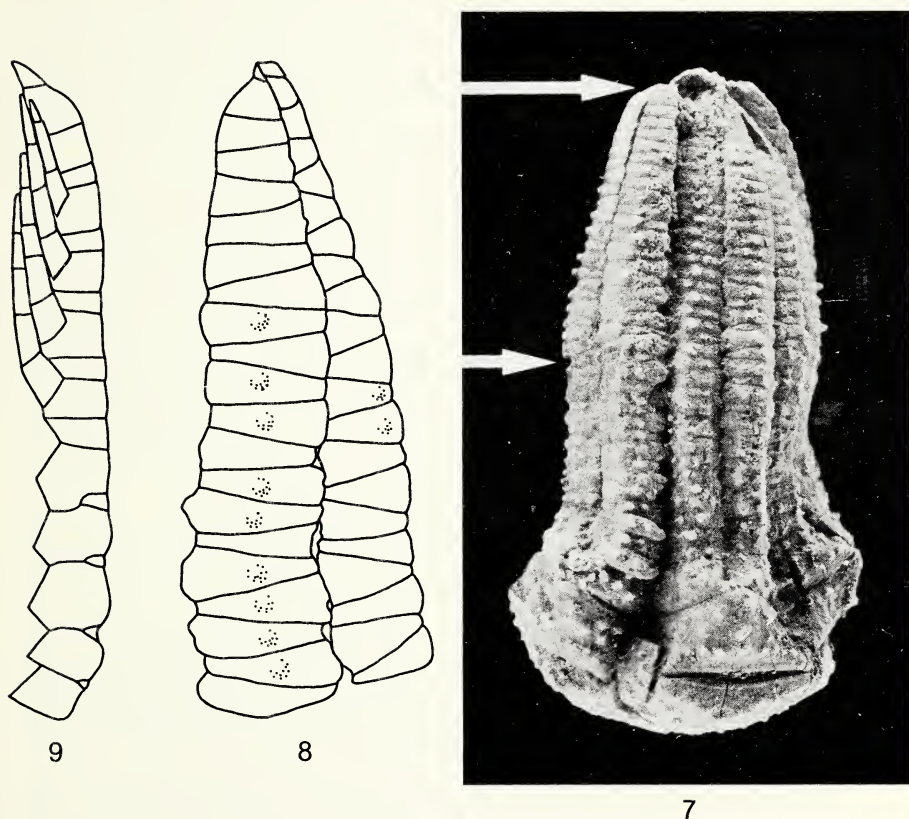
Now it is of great interest that this final stage in sutural contact seems nearly to have been attained by the cup plates of the holotype of *Diphuicrinus faustus* Moore and Strimple, OU 7511. Portions of the articular surfaces of the D radial and the DE basal of this specimen are exposed because the E radial has slipped inward. Both the interr radial and the radial-basal suture faces show surfaces that are practically flush, with elevations occupying the places of the fossae and crenellae showing along the ridges.

The arms of *Diphuicrinus* are known from two specimens, both attributed to *Diphuicrinus faustus* Moore and Strimple by those authors (1973). The arms of the holotype, OU 7511, were illustrated by Moore and Strimple (1973, pl. 14, fig. 1a; pl. 15, fig. 4a). The crown of the paratype of *D. faustus*, OU 4597, was figured by Strimple and Knapp (1966, pl. 36, figs. 1, 2) but the specimen, as depicted more recently by Moore and Strimple (1973, pl. 14, figs. 1b, 1d) no longer retains all of the surface detail of the arms, probably because of rash use of an air abrasive machine in preparation.

Study of these two specimens gives support to my previous suggestion (Burke, 1970, p. 9-10) that mature individuals of *Diphuicrinus* would be found to have biserial arm structure. In the midregions of the arms of these two crowns of *Diphuicrinus faustus*, biseriality appears to be already under way. The secundibrachs are quite cuneate; some of them are reduced to feather edges on the antipinnular side and do not extend the full width of the arm. But this is not fully apparent in external view, because the pinnular ends of some of the brachs are intruded between the pinnular ends of brachs of adjoining arms, which makes for a remarkably robust interlocking mechanism, but the interlocking brachs conceal the underlying structure of the arm. It is only the external portions of the brachs which mesh with and slightly overlap the brachs of adjoining arms. This is evident when the arms are separated. Actually, at depth, subjacent and superjacent pinnular ends of some of the secundibrachs are in

contact, and where they are in contact they fence off the tips of the antipinnular wedges, preventing them from extending the full width of the arm.

I have attempted to illustrate the arm structure of the holotype of *Diphuicrinus faustus*, OU 7511, in Figures 7, 8, and 9. In Figure 7, a right posterior view of the crown, the interlocking secundibrachs are shown. Notches are evident in the right side of the arm of the D ray, which is elevated above and does not mesh with the adjoining arm. The region between the arrows on the left side of the figure includes the portions of the arms of the D ray which are illustrated in Figures 8 and 9.



Figures 7-9. *Diphuicrinus faustus* Moore and Strimple. Holotype, OU 7511. Fig. 7, right posterior view of crown, x2. Arrows delimit portions of D ray illustrated in figs. 8 and 9. Fig. 8, external view of portions of both arms of D ray, x 4.6. Fig. 9, lateral view of portion of left arm of D ray, x 4.6.

The proximal secundibrachs of these arms of the D ray of OU 7511 are not satisfactorily preserved, consequently in Figures 8 and 9 only that part of the left arm beginning with the 15th secundibrach, and of the right arm the portion originating with the 17th secundibrach, are illustrated. Neither arm is quite complete distally. In Figure 8, an external view, both arms display the notches between secundibrachs, which become increasingly prominent proximad; distad the notches are less distinct and are not evident on the terminal parts of the arms. The left arm interlocks with the right, but it is free on the left side, because the right arm of the E ray is displaced and lies a greater depth. On this free side of the left arm it is evident that the antipinnular ends of the secundibrachs are exposed laterally, but there is no indication of the extent of their exposure at depth. In Figure 9, the extent of their lateral exposure is evident.

Figure 9 is a lateral view of this same part of the left arm of the D ray. Distad, some of the pinnules are preserved. But proximad lies the region of greatest interest, for here are exposed the pinnular ends of five secundibrachs with subjacent and superjacent surfaces in contact at depth. External to the junctures of the pinnular ends of these secundibrachs, four antipinnular tips of secundibrachs are seen, cut off from lateral exposure at depth, and progressively decreasing in size and extent of lateral exposure proximad (an indication that the antipinnular sides of the secundibrachs were being resorbed). There seems no escaping the conclusion that this arm was becoming biserial, and in fact exhibits biseriality in this region, where five successive secundibrachs on one side are in contact and pinnulate. In advance of this region the antipinnular ends of secundibrachs intervene between pinnular ends in typical uniserial fashion, and a few notches are evident. It is apparent that the interlocking structures of these arms were developed before the attainment of biseriality.

Burdick and Strimple (1973) have demonstrated that arms of fully mature specimens of *Phanocrinus* attain a stage of incipient biseriality, with all the brachs on each side pinnulate, but the arms are not biserial in any strict sense of the word. The cuneate brachs of *Diphuicrinus* are far more advanced than those of *Phanocrinus*, but whether any species of *Diphuicrinus* ever acquired biserial arms comparable to those of *Delocrinus*—or to those of Morrowan contemporaries of *Diphuicrinus*, such as *Endelocrinus*, remains to be demonstrated.

Whatever its ultimate assignment, *Diphuicrinus* is quite evidently a valid and distinct genus. Apparently the taxon is composed of species remarkable for their slow attainment of maturity, as demonstrated by the dorsal cup, which in some specimens appears literally to be "falling apart at the seams," and also by the arms, which in the two crowns that are known show only the beginnings of biseriality, although Strimple and Moore (1971) regarded one of them (OU

4597) as "young but mature." Another feature of *Diphuicrinus*, the coarse ornament, suggested "specialization" to Strimple and Knapp (1966). Coarse ornament does not characterize all of the species, but when present it is so marked that it might better be regarded as evidence of overspecialization. In general, there is much about *Diphuicrinus* that seems to me to indicate a crinoid stock in decline; something akin to phylogerontism appears to be in evidence here. I am inclined to view the taxon as a sterile offshoot of the *Phanocrinus* stock, which gave rise to no other Pennsylvanian genera, and which probably became extinct in Desmoinesian time. I consider it to be the sole member of the family Diphuicrinidae, as did Strimple and Knapp (1966). In view of the various unique characteristics of *Diphuicrinus*, the family deserves full recognition. However, it was originally assumed that *Diphuicrinus* was distinguished by uniserial arm structure, and this was the sole basis for establishment of the family. It is now evident that uniseriality simply represents a stage in the ontogeny of the diphuicrinid arm and does not constitute grounds for family distinction.

Almost any attempt to clarify the relationship of *Diphuicrinus* to several other genera contemporary with it would involve detailed taxonomic discussion beyond the scope of this paper. Nevertheless, one instance of generic confusion relates directly to *Diphuicrinus* and needs citation here. It stems from Strimple's (1961) proposal of the genus *Graffhamicrinus*, with *Graffhamicrinus acutus* as the type species. This crinoid is an ornate form, bearing a few superficial nodes on the cup plates and brachials; otherwise there is little to distinguish it from smooth-plated species of *Delocrinus*. Strimple founded his genus, and distinguished it from *Delocrinus*, on the basis of surface ornament of various types. Inasmuch as surface ornament alone, such as typifies *Graffhamicrinus acutus*, is not regarded by most crinoid authorities as sufficient grounds for generic distinction, I have refused to recognize *Graffhamicrinus* as a valid genus (Burke, 1966, 1970), relegating it to synonymy under *Delocrinus*, and continue to advocate its suppression.

However, within the omnium-gatherum of species which Strimple included under *Graffhamicrinus* there are some which in addition to surface ornament, show diagnostic features which entitle them to recognition as representatives of distinct genera. One of these was originally described as *Delocrinus aristatus* by Strimple (1949). Probably this species, more than any other, has been regarded as the connecting link between *Diphuicrinus* on the one hand and *Delocrinus* (= *Graffhamicrinus*) on the other. Of this taxon Pabian and Strimple (1974, p. 15) state: "*Graffhamicrinus aristatus* appears to be a very primitive representative of this genus. The radial facets, contour of the cup, and attitude of the anal plate strongly suggest a relationship to *Diphuicrinus* Moore and Plummer." I have recently examined the holotype of this species, an incom-

plete dorsal cup, USNM S 4690, and find it a typical example of *Diphuicrinus*; it shows a steep-walled basal impression, tips of radials in the basal plane, and a distinct forefacet. In lateral profile it resembles OU 6446, the specimen figured by Strimple and Moore (1971, figs. 9-11) and identified as *Diphuicrinus coalensis* ? Strimple and Moore. It also resembles OU 6445, the holotype of *Diphuicrinus coalensis*, in showing a much reduced stem. I am herewith designating the species *Diphuicrinus aristatus* (Strimple, 1949) comb. nov. If this species, or any other species of *Diphuicrinus*, is assumed to be either closely related or ancestral to *Delocrinus* (= *Graffhamicrinus*) I fail to find evidence to support that assumption.

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MAMMALS UTILIZED AS FOOD BY OWLS IN REFERENCE TO THE LOCAL FAUNA OF NORTHEASTERN OHIO

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ABSTRACT

Food habits of 6 species of owls living in northeastern Ohio were studied between 1949 and 1969 by pellet and stomach analyses. Small mammals constituted the bulk of the diet. In a sample of 1839 pellets of the Barn Owl from 5 counties, 96.86% of the food consisted of 3 species (*Microtus pennsylvanicus*, 77.27%; *Blarina brevicauda*, 16.94%; *Peromyscus leucopus*, 2.65%). Altogether, 14 species were utilized. These constituted 50% of the small mammal fauna of this area. Limited data indicate that the Great Horned Owl, Barred Owl, Long-eared Owl, and Screech Owl utilized essentially the same species, but the larger owls took more cottontails than the smaller owls. A sample of 85 pellets of the Short-eared Owl living at a city dump produced a different result, with 96.3% of the food consisting of introduced pest species—the Norway Rat (*Rattus norvegicus*, 75.9%) and the House Mouse (*Mus musculus*, 20.4%), with very little utilization of the common wild species of small mammals.

INTRODUCTION

Food habits of owls have been studied in northeastern Ohio over a period of 20 years by the analysis of disgorged pellets and stomach contents. For the 6 species of owls studied, small mammals constituted the bulk of the diet for each. While many studies have been published on pellet analyses for Barn Owls, this report gives stress to the relation of prey species to the available mammalian fauna.

Publications of food habits of owls in the area of the present study have been issued by Stupka (c. 1932) and Phillips (1951) for Ohio; by Price (1942)

for northwestern Ohio and northeastern Indiana; by Kirkpatrick and Conway (1947) for Indiana; by Wilson (1938), Wallace (1948), and Reed (1959) for Michigan; and Pearson and Pearson (1947) for Pennsylvania. The Wallace report (1948) is the most complete for this area and contains an excellent bibliography on the Barn Owl, including food habits.

The most intensive study for this report was made on the Barn Owl (*Tyto alba*), formerly a common species, but now becoming rare in the area. Williams (1950) classified the Barn Owl as a "not uncommon permanent resident." Formerly, the writer and his students banded Barn Owl nestlings and collected pellets in many barns of northeastern Ohio. In recent years, however, no Barn Owls were reported to the *Cleveland Bird Calendar* from 1964 until 13 December 1967, when one was seen by B. P. Bole, Jr., at Kirtland Hills. During the annual Christmas Bird Counts reported in *Audubon Field Notes* and *American Birds*, only 2 records of Barn Owls are given for northeastern Ohio since 1964. The exceptions were single birds at Burton and Mentor in January 1976.

RESULTS

A total of 1839 pellets collected from 5 counties of northeastern Ohio contained 5586 mammal skulls, which were identified through the keys of Katz (1941) and Glass (1958). This averages approximately 3 skulls per pellet, the same found by Wallace (1948) in his sample of 6742 pellets. Fourteen species of small mammals were included in the sample (Table 1). The two most common prey species, *M. pennsylvanicus*, the Common Field Mouse, and *B. brevicauda*, the Short-tailed Shrew, together account for 94.21% of the prey. The top 3 species account for nearly 97% of the food, while the remaining 11 species make up only slightly more than 3% of the food. The Meadow Mouse, *M. pennsylvanicus*, was the chief item of food for the Barn Owl in this area. This species comprised nearly 80% of Ohio pellets analyzed by Stupka (c. 1932) and a little over 85% reported by Phillips (1951). Both of these studies, however, found *B. brevicauda*, the Short-tailed Shrew, comprised a little more than 6%, in contrast to the present study, which found that it comprised nearly 17%. While Price (1942) found a similar utilization of the Meadow Mouse, he found the Short-tailed Shrew made up only 4% of the food in Williams County, Ohio, but he found *Cryptotis parva*, the Least Shrew, made up 27% as the second most important food item in that area. Wilson (1948) found *M. pennsylvanicus* and *B. brevicauda* to be the first and second most important in his study in Michigan, although the latter was less important than in the present study for northeastern Ohio. Wallace (1948) found a larger percentage for *M. pennsyl-*

TABLE 1

Mammals Found in Barn Owl Pellets—Northeastern Ohio—(1949–1969)

Species	Lorain	Medina-Summit	County Portage	Stark	Totals	%
<i>Microtus pennsylvanicus</i>	618	723	1672	1303	4316	77.27
<i>Blarina brevicauda</i>	92	133	512	209	946	16.94
<i>Peromyscus leucopus</i>	6	18	25	99	148	2.65
<i>Zapus hudsonius</i>	3	10	36		49	0.88
<i>Rattus norvegicus</i>	1	2	15	9	27	0.48
<i>Sorex cinereus</i>	3	3	15	6	27	0.48
<i>Mus musculus</i>	2	2	15	9	28	0.50
<i>Condylura cristata</i>		1	16	1	18	0.32
<i>Cryptotis parva</i>	3		4		7	0.13
<i>Eptesicus fuscus</i>	1		6		7	0.13
<i>Sylvilagus floridanus</i>			1	5	6	0.11
<i>Parascalops breweri</i>			3	1	4	0.04
<i>Sorex fumeus</i>		1		2	0.04	
<i>Mustela nivalis</i>		1			1	0.02
Totals	729	894	2320	1643	5586	
Number of Pellets	307	283	710	539	1839	

vanicus (84.97%), but a smaller percentage for *B. brevicauda* (6.53%), in his study in Michigan, than reported here, but these 2 species made up the bulk of the diet in Michigan as well as in Ohio.

Pellets and stomach contents of the Great Horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), Long-eared Owl (*Asio otus*), and Screech Owl (*Otus asio*) indicate utilization of the same common species of mammals used by the Barn Owl. However, insufficient data were acquired to establish meaningful ratios of prey. The only notable difference is the more common occurrence of the Cottontail Rabbit in the diet of the larger species of owls.

A sample of 85 pellets of the Short-eared Owl (*Asio flammeus*) collected 8 February 1956 from an owl living at the Cleveland dump demonstrated an unusual relationship in the food of the owls. Synder and Hope (1938) found *M. pennsylvanicus* to make up the vast bulk of the diet of the Short-eared Owl. The House Mouse, *M. musculus*, represented only 0.1% of the prey in their study made in the Toronto region. Hendrickson and Swan (1938) found the winter food of this owl in Iowa to be almost entirely *M. pennsylvanicus* and *P. leucopus*. Terres and Jameson (1943) also found *M. pennsylvanicus* to make up the bulk (82.17%) of the diet for this owl near Perry City in New York, while *M. musculus* composed nearly 12%. Stegeman (1957) found *M. pennsylvanicus* to make up 97.2% of the winter food while *M. musculus* accounted for only 0.15% and *R. norvegicus* only 0.07% in central New York. Reed (1959) found only *M. pennsylvanicus* (74.1%) and *P. leucopus* (25.9%) in the sample he studied in Michigan. In this study there were 41 skulls (75.9%) of *R. norvegicus*, and 11 skulls (20.4%) of *M. musculus*. There were only 2 skulls of *M. pennsylvanicus*. This is a reversal of the usual ratio and is a reflection of the specialized habitat of this particular owl. While most owls live in rural habitats, this one lived in a city dump.

DISCUSSION

Five orders of small mammals were utilized by the owls examined in this study. Rodentia (5 species) and Insectivora (6 species) composed over 99% of the food. Chiroptera, Lagomorpha, and Carnivora were each represented by a single species.

Phillips (1951) listed many local species of small mammals not utilized by the Barn Owl in his area. Bole and Moulthrop (1942) recorded 20 species of small mammals from northeastern Ohio. Only half of these were found in the diets of owls studied here. The other half, however, are either uncommon species for the most part, or they are chiefly diurnal in their activities. Dexter (1955) recorded 19 species of small mammals on the Kent State University

campus in Portage County, Ohio. Again, only half of these were found in owl pellets collected in that area, and those species not utilized are relatively uncommon and, in some cases, diurnal in their activities.

Pearson and Pearson (1947) concluded that, "Neither owls nor trappers catch a representative sample of the small mammal population." Stegeman (1957) also concluded that the prey found in pellets did not reflect the relative abundance of the prey species in nature, and Weller et al. (1963) demonstrated that "Mammal trapping in the owl roosting areas produced quite different data on species composition of the mammalian fauna than was implied from the remains in owl pellets."

Apparently, owl pellet analysis cannot be used to give reliable data on the relative abundance of local small mammals. It is clear from the present study, however, that the great bulk of mammals utilized by local owls for food consists of only 3 common species, with only 50% of local species in the area being utilized.

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LIPID DEPOSITION IN THE HOUSE SPARROW AND RED-WINGED BLACKBIRD

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ABSTRACT

In Central Michigan the mean fat to dry-lean weight ratios of juvenal and adult House Sparrows and Red-winged Blackbirds ranged from 0.09 to 0.35 during the summer and fall of 1973. The lipid index of adults was lowest during the breeding season and highest in the fall. Female red-wings migrated by early September shortly after completion of the postnuptial molt with no apparent increase in fatness. In late autumn other red-wings began premigratory fattening and increased their fat to dry-lean index from 0.16 in late October to 0.35 in mid-November. The sparrow fat index increased gradually from 0.09 early in the season to 0.17 in November.

Odum (1960), Caldwell et al. (1964), and Johnston (1966) have stated that some avian species begin migration in a relatively lean state and gradually increment their fat reserves through hyperphagia as they move toward their spring breeding areas or fall wintering grounds. In contrast, nonmigratory species presumably do not exhibit any appreciable vernal or autumnal increase in body fats.

In the present study amounts of whole body lipid values were compared between the migratory Red-winged Blackbird (*Agelaius phoeniceus*) and the nonmigratory House Sparrow (*Passer domesticus*). Whole body lipids were measured through the summer and into the fall migratory season.

METHODS

Collections of the two species were made in Isabella County, Michigan, from May into December 1973 with a shotgun and number nine shot. The

blackbirds ($N = 130$) were taken from both upland and marshland habitats and the sparrows ($N = 88$) were collected near human dwellings or farm outbuildings. All specimens were weighed and then frozen until the time of analysis.

Skull ossification was used to separate birds of the year from older birds (Nero, 1951; DeHaven et al., 1974). Each specimen was dissected, the sex determined, and the gut and crop contents removed before fat extraction. The fat extraction technique involved the use of a food blender with petroleum ether and ethyl alcohol solvents and is described elsewhere (Matson and Caldwell, Kirtlandia, No. 26).

RESULTS

Fledged immature House Sparrows were of a smaller body mass than the adults. The mean dry-lean weight of the fledglings at 6.5 ± 0.12 (1 standard error of the mean) grams was significantly smaller than the adults 7.61 ± 0.06 grams ($P < 0.01$). However, since total body fats averaged 0.96 grams for each group, the immature birds had a higher fat to dry-lean ratio (0.15) than did the adults (0.12) because of a smaller dry-lean body mass ($P < 0.05$).

A fat to dry-lean comparison in the red-wing is more complex because this species exhibits sexual dimorphism and premigratory fattening. The females average 11.18 grams of dry-lean weight and were smaller than the males at 18.68 grams ($P < 0.01$).

With regard to age differences, immature female red-wings were significantly smaller in dry-lean body mass at 10.17 grams than adult females (11.49 grams, $P < 0.05$), as would be expected. Likewise, immature males at 16.70 grams were smaller than the adult males at 19.34 grams ($P < 0.01$). There was likewise a tendency for immatures to be more obese than the adults. During the summer and early fall months the 0.18 fat index of immature red-wings of both sexes combined was significantly higher than the 0.14 value found in the adults ($P < 0.01$). Just prior to migration, the ratio of fat to dry lean of the immatures rose to 0.29 but there was no difference from the ratio value of the adult birds at 0.27 ($P > 0.50$).

Adult House Sparrows in the early part of the nesting season had a fat index of 0.09 with a variance of only 0.0002 (Fig. 1). In the middle and later parts of the nesting season the variance was much larger ($S^2 = 0.003$), but the mean index (0.12) had not risen significantly ($P < 0.10$). By late October, after the postnuptial molt, the index had increased to 0.17 while the variance had decreased to 0.0005. The postnuptial fat index was markedly higher than the early nesting season index ($P < 0.001$). The fat index of the immatures averaged 0.14 throughout most of the nesting season, but in early October it declined to 0.11 before increasing to the same value (0.17) as found in the adults in late October.

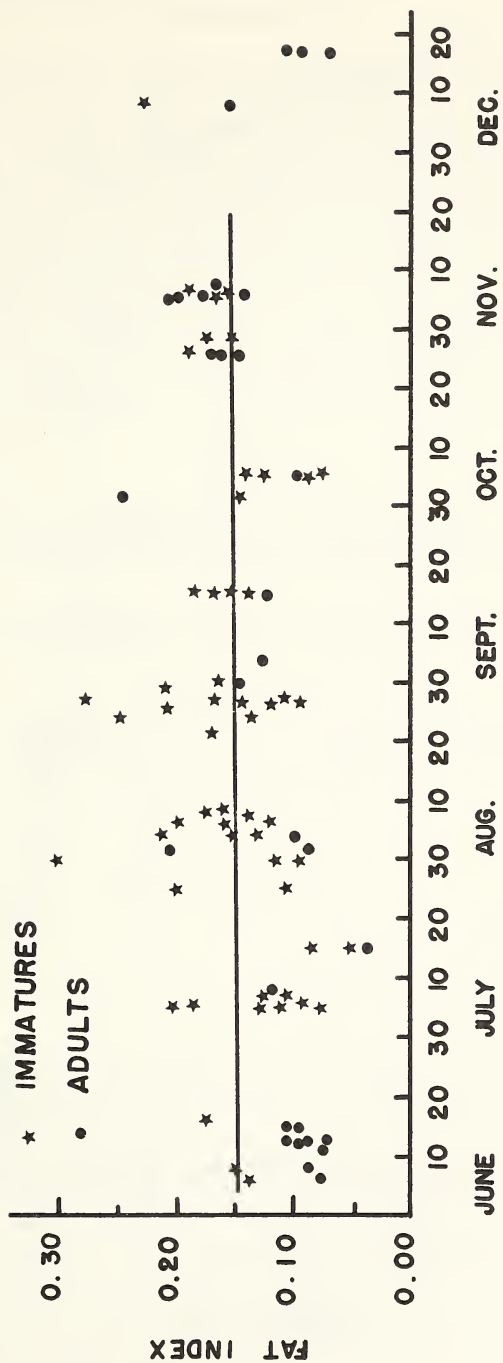


Fig. 1. Changes in the fat index of adult and juvenile House Sparrows in Central Michigan during the summer and fall of 1973.

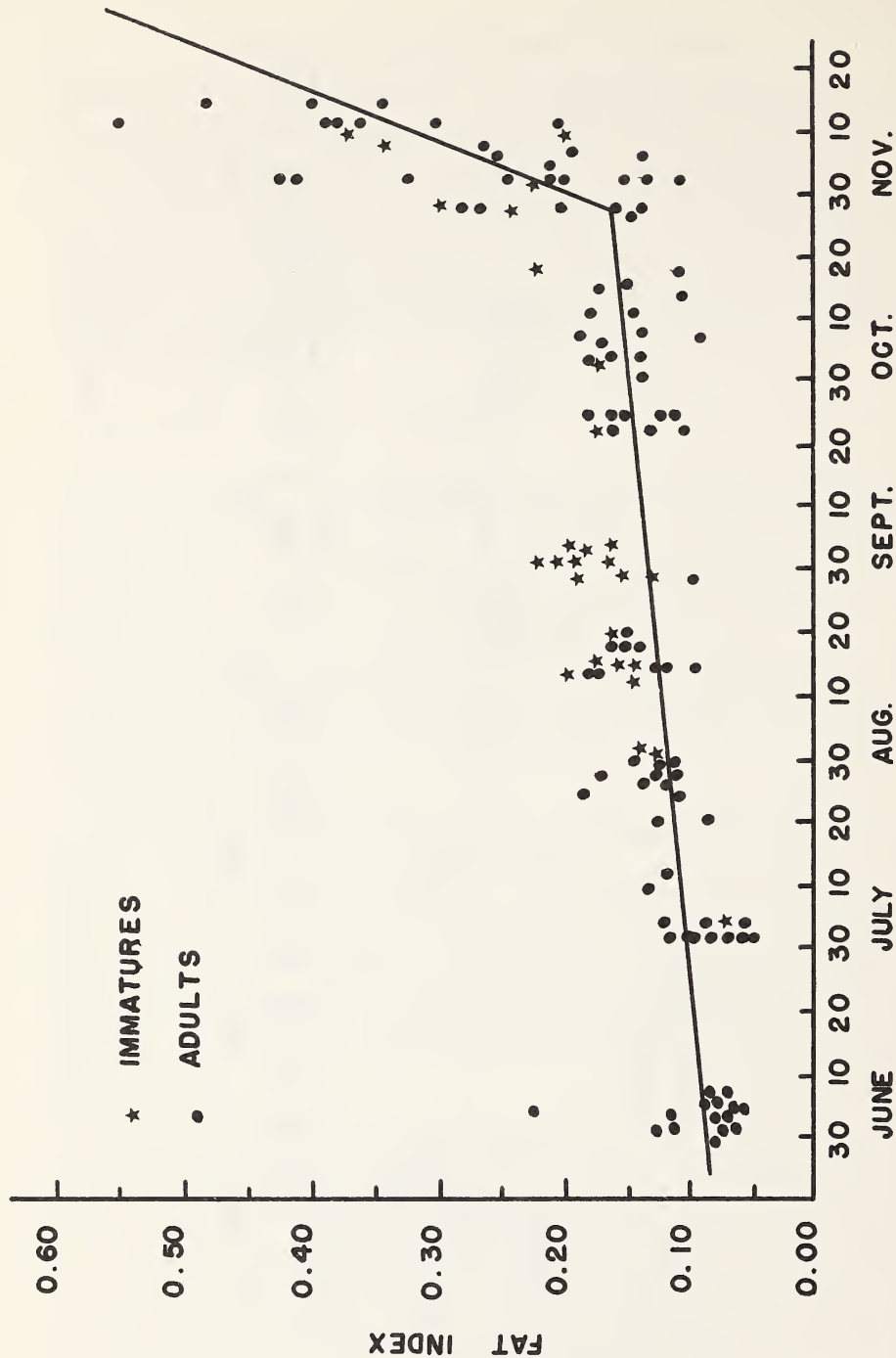


Fig. 2. Changes in the fat index of adult and juvenile Red-winged Blackbirds on their breeding grounds in Central Michigan during the summer and fall of 1973.

The 0.09 fat index for adult red-wings during the June and early July nesting season (Fig. 2) was almost identical with the index of the adult House Sparrows ($P > 0.50$). Then by 15 August the red-wing index had risen to 0.14, where it remained relatively constant until the start of the fall premigratory fat build-up beginning about 27 October. The variance of the index throughout the above mentioned interval was moderate ($S^2 = 0.0009$). Then, between 27 October and 11 November, the index rose rapidly from 0.16 to 0.35. The linear regression equation for the increase of fat in grams per day for adult Red-winged Blackbirds during this period of rapid premigratory fattening is $Y = 0.27X - 36.78$ ($S^2 = 0.009$). In other words, 0.27 grams of fat were stored per day for approximately 15 days, at which time the migrants departed.

TABLE 1

Comparison of Major Body Components of Juvenal and Adult House Sparrows and Red-winged Blackbirds

Age	House Sparrow				
	Mean Dry-lean Weight (Grams)	Fat (Grams)	Fat Index	Water (Grams)	Water Index
Juvenal	6.5	1.0	0.2	20.1	3.1
Adult	7.6	1.0	0.1	21.0	2.8
Age	Red-winged Blackbird				
	Mean Dry-lean Weight (Grams)	Fat (Grams)	Fat Index	Water (Grams)	Water Index
Juvenal	15.1	3.1	0.2	42.2	2.8
Adult	17.3	3.0	0.2	43.1	2.5

The data that have been analyzed in this study are linear rather than discrete in nature. For summary purposes, however, a set of discrete data in tabular form is valuable for reference (Table 1). Notice in Table 1 that water is also a variable body component. The water index (water weight divided by dry-lean weight) is lowest in the adults. The 3.1 index of immature sparrows is higher than that of the immature red-wings (2.8) and other avian species for which water indices have been determined. For example, Ricklefs (1967) found the index of fledgling Barn Swallows to be about 2.3 and for Dickcissels it is about 2.3 (Zimmerman, 1965). The value for adult House Sparrows (2.8) and adult Red-winged Blackbirds (2.5) is quite close to the index of 2.6 in Long-billed Marsh Wrens (Kale, 1965).

DISCUSSION

Both House Sparrows and adult Red-winged Blackbirds were relatively lean with a low fat index (0.09) and low variance during the early part of the nesting season (Figs. 1 and 2). The low index and variance in the adult is probably related to a uniformly high expenditure of energy in nesting activities once breeding and caring for the young begins. Once the first clutch has been raised, however, the variance increases as some adults increase their lipid reserves. Increased variance in the ratio of fat to dry-lean during the middle and latter part of the House Sparrow nesting season should be expected since not all adult birds breed the same number of times (Weaver, 1943) nor is the second breeding as synchronized as the first breeding. Folk and Novotny (1970) in their year-long study of the body weight of the House Sparrow noted that the body weight decreased in May. They attributed this loss to parental care for the young of the first clutches. In June, however, they found that the body weight increased in accordance with the production of sexual products for the next breeding. It seems that in addition to the increase in sexual products our data indicate that some of the body weight increase is due to the increase in fat reserves following the period of parental care for the young, especially in the individuals that breed only once during the season. Similarly, the index of the red-wings increased after the period of parental care ended in early July.

By late October, after the breeding season was finished and the postnuptial molt had been completed, the ratio of fat to dry-lean of the House Sparrow was again uniform. Folk and Novotny (1970) found that by October the body weight of the male and female components of their sample had risen significantly over that of the birds taken during the breeding season. They attributed this increase in body weight to the increase of fat prior to the winter months. This study indicates that their proposal is correct and that House Sparrows do indeed increase their fat reserves prior to the winter season. Note that the 5 House Sparrows collected in December were not involved in the data analysis or interpretation since they were collected after the red-wings had departed for the winter.

Molting requires energy and could result in a drop in the fat index if food intake is rather low. The effect of the postnuptial molt on the fat index of the adult House Sparrow is uncertain. Adults were found replacing flight feathers from about the middle of August through the latter part of October. The data on adults during this period are, however, too few to make any meaningful analysis.

Adult red-wings were observed molting from late July into the early part of October. A statistical comparison of the fat index between molting adults and

nonmolting adults reveals no significant differences between the two groupings ($P < 0.40$). Unfortunately, only 4 adult birds were observed not molting during this period. Likewise, the sample number ($N = 2$) of nonmolting immatures was too small to warrant a comparison with molting immatures.

It should be noted that after 1 September only two female red-wings were collected. Shortly after completing the postnuptial molt, both adult and immature females migrated to other areas. A comparison of the fat indices between the last two females collected in September (0.19) with the only two females collected in November (0.34) reveals that females found in the area late in the fall had increased their fat reserves considerably over those leaving earlier. The fat index of 0.34 found in the November females is comparable with the 0.27 value found in adult males during this premigratory fattening period. In other words, most female red-wings begin some form of migration early in the fall or late summer after completion of the postnuptial molt, and they do so without increasing their fat reserves to any appreciable degree. Yet those few females that are found in the area in the late fall increment their fat depots to levels equal with those of males, which normally migrate in November.

During the premigratory fattening period that began around 27 October the fat index of the Red-winged Blackbirds increased from 0.16 to 0.35, thus doubling in value from the summer period. The index values of 0.29 and 0.27 for immature and adult male red-wings during premigratory fattening were not significantly different ($P > 0.50$). The equation expressing the relationship between the fat index and time during premigration for both age groups is $Y = 0.01X - 1.11$, where Y is the fat index and X is the number of the collection day based on 31 May as day one. In other words the ratio of fat to dry-lean weight increased 0.01 each day from 27 October to 14 November. Thus, as mentioned earlier, an average of 0.27 grams of fat were added to the lipid depot each day throughout the premigratory fattening period. For comparison, Morton et al. (1973) estimated the rate of fattening of transient White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) as 0.3 grams per day. He also estimated the rate of fattening of captive *Zonotrichia leucophrys oriantha* to be about 0.1 grams per day for the few days following the molting period, and preceding the autumn migration. From the data in Table 1 of Norris et al. (1957) it is possible to calculate the rate of lipid accumulation of a transient flock of Ruby-throated Hummingbirds during a period of intense preflight fattening. The mean fat content increased from about 1.07 grams on 16 September to a value of 2.18 grams on 23 September. In other words, fat was deposited at a rate of 0.16 grams per day throughout a seven day period before the birds left the area. Of course the Ruby-throated Hummingbird, by virtue of its small size, does not need to accumulate as much fat as the red-wing. But for comparative

purposes it is interesting to note that the red-wing, which has a dry-lean weight 18 times that of a Ruby-throated Hummingbird, adds almost twice as much fat per day. It is important to realize that the premigratory fattening period of the red-wing lasts about 16 days in contrast to the amazingly short time of about 7 days in the transient Ruby-throated Hummingbird population studied by Norris.

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LIPID DEPOSITION IN NESTLINGS OF THE HOUSE SPARROW AND RED-WINGED BLACKBIRD

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ABSTRACT

It is well known that lipid depots serve as an energy source for birds during migratory flight. Furthermore, studies by Wolfson (1954), Odum and Connell (1956), King and Farmer (1959) and others have shown that lipid volumes vary from one phase of the annual life cycle to the next. Little of the work on avian lipids to date, however, has been concerned with nestlings. According to Brenner (1964), nestling Red-winged Blackbirds (*Agelaius phoeniceus*) deposit about 75 mgms per day. Brenner's measurements were made from body organ sections and the major lipid depots.

In the spring and summer of 1973 nestlings of the House Sparrow (*Passer domesticus*) and Red-winged Blackbird were collected in Isabella County of central Michigan. The House Sparrow as a nonmigrant serves as a basis of comparison with the Red-wing which is a medium-range migrant. The Red-wing winters in the United States as far south as Florida and Texas.

METHODS

An entire clutch of nestlings was removed at each nest site rather than removing part of a clutch and thus increasing the quantity of nutrient available to the remaining nestlings. We collected 62 House Sparrows and 46 Red-wings. Weights were taken after collection and specimens were frozen in plastic bags until the time of analysis. Nestlings were aged to the nearest day by using the weight and feather tract development criteria of Weaver (1942) and Williams (1940). Each specimen was dissected, the sex determined, and the gut and crop contents removed before fat extraction.

The fat extraction technique involved the use of a food blender with petroleum ether and ethyl alcohol solvents. Each specimen was covered with alcohol and then macerated in the blender for 45 seconds. Petroleum ether was used to wash the residue into a beaker, which was then placed over a steam bath for several minutes. The two-solvent mixture was subsequently filtered through a strainer and filter paper into a separatory funnel. The residue that was trapped in the strainer was again extracted with petroleum ether in the beaker, heated, and filtered through the filtering system a second time. A total of 10-22 volumes of solvent was used relative to body mass for the extraction process. A biphasic system subsequently resulted upon acidification of the two-solvent mixture (Cratin, 1970). The ether phase, containing the fat, was drawn off, whereas the alcohol phase was washed 2-3 times with petroleum ether. All ether phases for each specimen were finally pooled and evaporated to near dryness. The concentrated fat was then transferred to a preweighed aluminum pan for drying over a steam bath. Final drying was achieved in an oven at 115°C for 12-18 hours. The dried weights of the residue on the filter paper and the residue on the strainer combined represents the dry-lean weight or nonfat dry weight. The method of Cratin (1970) when properly applied gives fat values virtually identical to results obtained by the popular Soxhlet method of fat extraction.

RESULTS

Nestling sparrows exhibited a linear relationship between fat and dry-lean weight as expressed by the equation $Y = 0.18X - 0.03$ (Fig. 1, line A). In other words, 0.18 grams of fat were added for each 1.00 gram of dry-lean weight increase in body mass. However, this line of best fit is separable into two stages, with a tendency for the smaller nestlings (Fig. 1, line B) to accumulate fat more slowly than the larger nestlings (Fig. 1, C) which have a dry-lean weight of 2.49 grams or greater ($P < 0.01$ between slopes). Small sparrows exhibited much less variance about the regression than did the large individuals (0.001 and 0.007 respectively). Notice that 2 nestlings in the lower right-hand corner of the figure were very lean when compared to all other nestlings of a similar dry-lean weight. The above 2 nestlings were not included in the calculations of the regression line. Each of the 2 lean nestlings came from a different clutch.

In contrast, the blackbird nestlings were considerably more variable in the rate of fat increment with respect to dry-lean weight (Fig. 1, line D). In spite of the large overall variance in nestling blackbirds, the smallest individuals of both species were very similar. The eight smallest Red-wings ($X = 0.67$ grams) had 0.06 grams of fat. Accordingly, the fat/dry-lean ratio was 0.09 and was

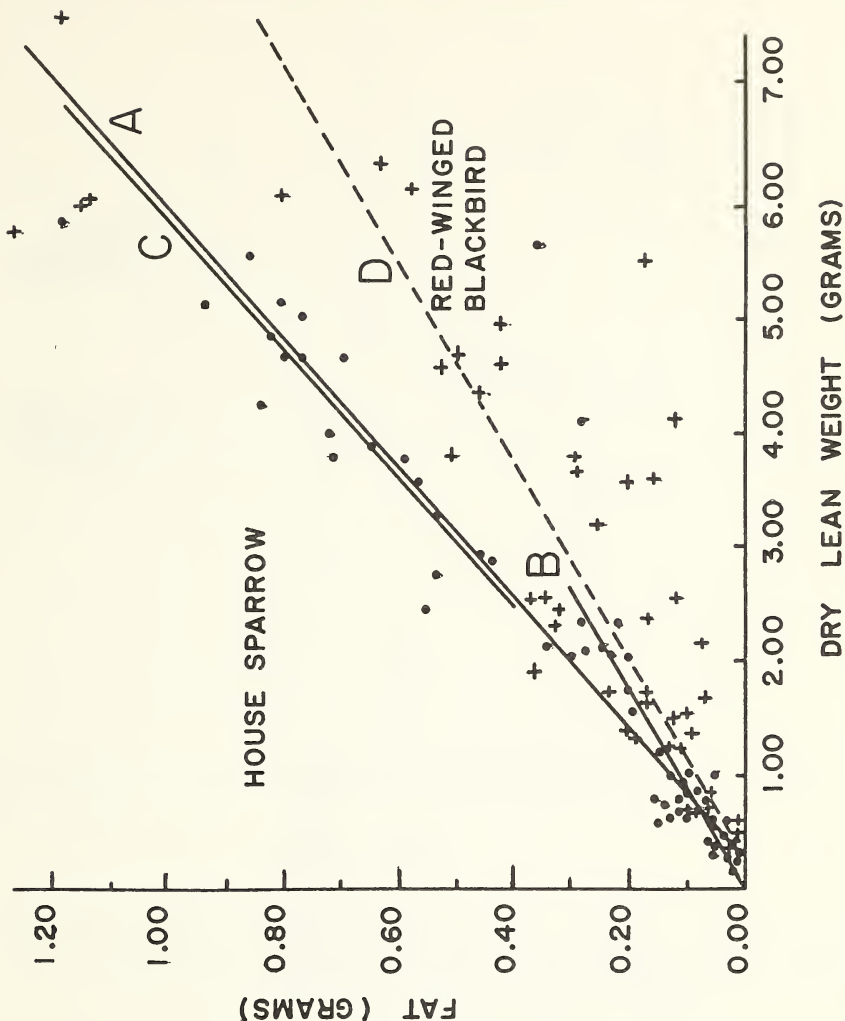


Fig. 1. Changes in the fat content of nestling House Sparrows and Red-winged Blackbirds as a function of dry-lean weight. The equation of the regression line describing all the House Sparrow data (line A) is $Y = 0.18X - 0.03$. The equation for nestling sparrows with a dry-lean weight of less than 2.49 grams (line B) is $Y = 0.12X - 0.00$, whereas the relationship of nestlings 2.49 grams and more in weight (line C) is given by the equation $Y = .17X - 0.01$. The equation of the regression line describing nestling Red-winged Blackbirds (line D) is $Y = 0.12X - 0.04$.

identical to that of the 8 smallest sparrows. The blackbird variance from the regression increased rapidly to a maximum in the 6.00 to 7.50 gram weight class, at which point body fat ranged from 0.58 to 1.15 grams. The overall fat

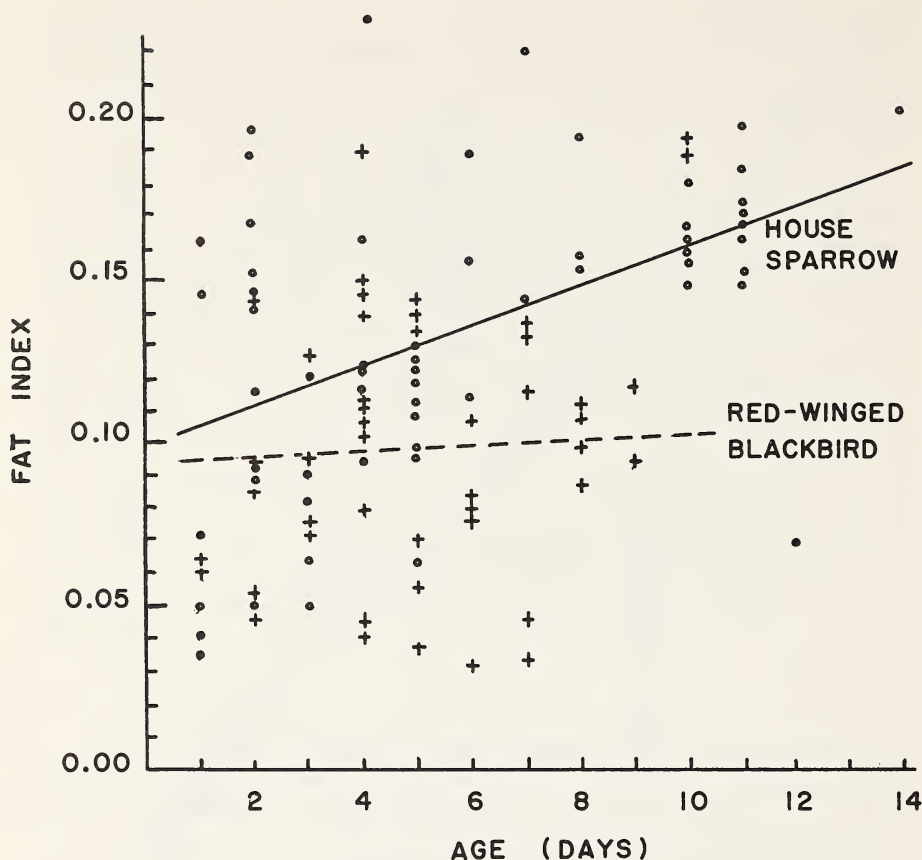


Fig. 2. Changes in the fat index of nestling House Sparrows and Red-winged Blackbirds as a function of age. The equation of the regression line describing the House Sparrow is $Y = 0.01X + 0.10$, whereas the equation describing the blackbird is $Y = 0.01X + 0.08$.

index equation for the blackbird is $Y = 0.12X + 0.02$ with a variance of 0.02. Thus, sparrow nestlings with a regression coefficient of 0.18 had one-third more lipid per gram of body mass than did the blackbirds at 0.12. An analysis of covariance between species regression lines reveals a significant difference between slopes (i.e., fat index, $P < 0.01$).

Our fat index versus age-in-days analysis shows a large scatter of data. This variance is partly related to the difficulty of aging nestlings more accurately than to within a 24 hour interval (Figure 2). The 0.002 variance for nestling sparrows during the first 6 days was twice as large as the 0.001 variance of the older individuals. By contrast, the blackbird nestlings exhibit no correla-

TABLE 1
Comparison of Mean Weights of the Major Body Components of House Sparrow
and Red-winged Blackbird Nestlings of Three Age Groups

Age (Days)	Dry-lean Weight (Grams)	House Sparrow			Water (Grams)	Water Index
		Fat (Grams)	Fat Index	Red-winged Blackbird		
1-5	1.1	0.1	0.1		8.5	7.7
6-10	3.3	0.5	0.2		17.9	5.4
11-15	4.8	0.8	0.2		20.8	4.3
				Red-winged Blackbird		
1-3	0.9	0.1	0.1		8.5	9.4
4-6	2.5	0.2	0.1		15.8	6.3
7-9	5.3	0.6	0.1		23.8	4.5

tion ($P < 0.10$) between fat index and age. In other words, the ratio of fat to dry-lean changed little during development. Variance in fat index is, however, large at all stages of blackbird nestling development.

Water is also a dynamic body component of developing nestlings (Table 1). As would be expected, the water content of both species increased with age up to the time of fledging. A water index (water content divided by the dry-lean weight), however, is often used to express body water content. Since the dry-lean mass increases at a high rate in developing birds, one can observe in Table 1 that the water index declines with age of the individual. In terms of total body mass, the water content of the sparrow and blackbird decreased from 87 and 89 percent respectively down to 79 and 80 percent. Body water of adult birds would likely approach 66 percent.

DISCUSSION

The fat to dry-lean ratio in nestling sparrows just prior to fledging was almost one-half higher than the ratio in Red-wing nestlings. The difference in fat between nestlings is probably related to the different time intervals spent in the nest by each species plus the size difference between species. House Sparrows fledge at about 14.4 days of age (Weaver, 1942). Body mass increases from 2.8 grams at hatching to about 26 grams at fledging for a growth rate of 1.6 grams per day. In contrast, female and male Red-wings respectively spend only 9.2 and 9.7 days in the nest (Holcomb and Twiest, 1970). The growth rate for females is 2.8 grams per day, whereas males grow at 3.0 grams per day. Body mass for the two sexes respectively increases from 5.0 grams at hatching (Williams, 1940) to 33 and 35 grams at fledging (Holcomb and Twiest, 1970). Thus both sexes of the blackbird achieve a larger body mass increment than the sparrows during a shorter time span (almost a twofold difference in growth rates). Since growth of the Red-wing nestling is relatively fast, it seems reasonable to find fat storage to be minimal. Energy intake in the blackbird is evidently channeled more into skeletal and nonfat tissue growth. In contrast, excess lipid deposition can occur in the nestling House Sparrow apparently because of its lesser energy demand for tissue growth.

The variance in the ratio of fat to dry-lean weight for the nestling House Sparrows (Fig. 1) was much lower for the nestlings under 2.49 grams than for those nestlings above that amount. Weaver (1942) suggests that as fledging approaches, the larger nestlings are found high in the nest and accordingly receive more food than do any smaller siblings. Since competition for food between siblings probably increases with age, it follows that some individuals receive more food than do others. As a result, some siblings would be able to

store more fat (higher fat index), thus possibly accounting for the increased variance observed in the larger nestling size cohorts.

Although the data on Red-wings are few in the 5.00 to 7.00 gram dry-lean weight category (Fig. 1), it appears that the rate of fat deposition increases just prior to fledging, thus making the regression line somewhat curvilinear. As mentioned earlier, Brenner (1964) employed different methods on nestling Red-wings and obtained results similar to those of the present study. According to Brenner, the amount of fat deposited per gram of body weight decreased up to day seven and then increased rapidly until the time of fledging.

The large variance encountered in the fat index of nestling House Sparrows 6 days and under in age was undoubtedly due to the difficulty in correctly aging individuals to within a 24-hour period. Weaver (1943) found that the first 2 or 3 eggs in a clutch were incubated for about the same length of time. The other eggs usually hatched 12 to 24 hours later but always within 48 hours. With such a large time interval between the hatching of eggs, the first nestlings to hatch have a competitive developmental advantage over their siblings with respect to begging food from the parents. The nestlings hatching later may receive enough food to sustain life and increase their body mass, but may not receive enough food to store much energy in fat depots. As a result, the fat index of the nestlings to hatch last would be lower than that in the nestlings to hatch first, and hence one observes a large variance in the data. It appears that the nestlings hatching later, however, catch up with their older siblings in fatness during the last half of the nestling period. This probably occurs because the rapid increase in body mass appears to slow after about 6 days (Table 1). Slowing of the growth rate of the older siblings would allow the younger nestlings to receive more food and deposit more fat, thereby achieving about the same fat index as their older siblings.

Fat index did not increase with age for red-wing nestlings, whereas the sparrow regression was quite significant ($P < 0.01$). Ricklefs (1967), while comparing the lipid index of nestling Barn Swallows to that of nestling Red-winged Blackbirds, was puzzled by the low levels of lipid reserves found in the nestling blackbirds. It seems likely that the low lipid levels observed by Ricklefs as well as those observed in the present study were due to the rapid increase in nonfat body mass. In Table 1 the index for sparrows increased from 0.08 to 0.16, whereas the blackbird fat index increased from 0.08 to only 0.11. As mentioned previously, nestling Red-winged Blackbirds display a very high growth rate, and, therefore, do not accumulate fat to any appreciable extent. If the energy intake is just adequate to promote tissue growth, then the ratio of fat to metabolic body mass will likely remain the same with time. Any excess energy results in fat storage and reflects either large food energy sources or only

moderate energy demands for tissue growth or a combination of these two factors. From Figure 2 it is evident that the Red-wing is of the first category with tissue growth being the highest metabolic priority, and the House Sparrow, with an increase in fat index with age, is of the second category, where surplus energy for fat storage is available.

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BENTHIC RECOLONIZATION PATTERNS IN THE VERMILION RIVER, OHIO

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ABSTRACT

Two recolonization studies were performed in the Vermilion River, Ohio, by planting invertebrate-free sedimentary "islands" in the substratum and then collecting them at predetermined intervals. Every macroinvertebrate taxon found living on the undisturbed sedimentary bottom appeared on the islands by the 5th week in the first study and by the 24th day in the second study.

Drift was likely an important source of organisms in the early stages of recolonization. Nevertheless, the taxonomic composition of the sedimentary islands was not entirely predicted by the total composition of the drift fauna.

Compared to the marine environment, the pattern of recolonization in the Vermilion River is not established mainly through reproductive events but rather by the relative mobility and abundance of the organisms involved. Also, the time involved in complete recolonization is much less for the Vermilion River. This rapid recolonization ability of lotic benthos helps insure survival of the various species by aiding their wide dispersal within their habitat.

INTRODUCTION

By a series of experiments in which he observed the recolonization by benthic macroinvertebrates of sedimentary "islands" planted on the sublittoral sediments of Long Island Sound, McCall (1977) conclusively demonstrated that studying recolonizing processes in aqueous environments can provide important insights into the structure and dynamics of benthic communities. Furthermore, he showed that such experiments can also provide information regarding the patterns and rates by which benthic communities recover from local disasters such as pollution events.

Like McCall's, most colonization or recolonization studies which are based in aquatic environments are generally concerned with macrobenthos (particularly invertebrates) and involve the marine realm. A summary of the scope and significance of many of these marine-based studies is currently being prepared (McCall et al., in *prepr.*). By contrast, there are noticeably fewer macrobenthos colonization or recolonization studies for freshwater environments. Those involving lentic environments are often concerned with changes in species composition, richness, and abundance that occur when a new lake is created or an existing dry lake refilled (e.g., McLachlan and McLachlan, 1971; Paterson and Fernando, 1969; McLachlan, 1975). Experiments based in lotic environments generally fall into one of the following three categories: 1) the recovery of benthos after pollution abatement (e.g., Brinkhurst, 1965; Crisp and Gledhill, 1970); 2) the colonization of introduced artificial or natural substrata as a means of benthic sampling (e.g., Mason et al., 1970; Coleman and Hynes, 1970; Glime and Cleman, 1972); and 3) the sources (i.e., by drift, upstream migration, etc.) of recolonizing organisms (Waters, 1964; Williams and Hynes, 1976). A single study involving macroinvertebrates was concerned with colonization patterns on artificial substrata in relation to the MacArthur-Wilson equilibrium model (Dickson and Cairns, 1972; see also MacArthur and Wilson, 1963). Lotic environments in general are not extensively studied in terms of macrobenthic recolonization.

The main purpose of this paper is to provide new information concerning little-known aspects of recolonizing processes involving lotic macroinvertebrates, including the sequence of appearance of different organisms during recolonization, the relative efficiency of various organism sources with respect to rates of recolonization, the time involved in a complete recolonization cycle, and the way in which the overall aspect of lotic recolonization is comparable to recolonization patterns in other environments. It is hoped that this information will not only provide a more comprehensive view of recolonization processes in aquatic systems in general, but will also provide a more complete understanding of how rapidly river beds may recover biologically from local disasters. Additionally, this paper presents the first published account of the dynamics of benthos of the Vermilion River, Ohio. The Vermilion is one of several similar, little-studied northern Ohio rivers that empty into Lake Erie. Information for this study was collected by the author during July-September 1975 from the Vermilion River, Ohio.

STUDY AREA

The Vermilion River arises in the community of Bailey Lake (Ashland Co.), Ohio, where it is the main outlet of Mud Lake (40° 57' N, 82° 21' W).

According to the Ohio Division of Water (1954), the river is 94.4 km long and drains an area of 703.4 km². The elevation at the source is 313.9 m, and the average fall is 1.5 m/km (all units here converted to the metric). The mouth of the river is in the town of Vermilion (Erie Co.), Ohio, where the river empties into Lake Erie. By interpolating figures received from the National Weather Service (personal communication) it is reasonable to estimate that the drainage basin of the Vermilion River receives about 86 cm of rainfall annually and that the average yearly temperature for the same area is approximately 10.4°C.

Excepting the last 5-6 km of the river, where it flows through suburban and urban areas and is in places noticeably polluted, all the upper reaches of the Vermilion flow through rural countryside where the chief pollutants are fine clastic sediments and fertilizers derived from agricultural operations. Inferring from the presence in the river of a variety of pollution intolerant organisms (e.g., diverse Plecoptera, Ephemeroptera, Trichoptera; Gaufin and Tarzwell, 1952, 1956; Beck, 1954), most of the upper reaches of the river are fairly clean.

The Vermilion's bed is a complex mosaic of sediments. Nevertheless, in the upper reaches of the river, the bottom is usually composed of one of two broad sedimentary suites. Where currents are more rapid, the bottom is largely composed of gravels consisting of shale, siltstone, or sandstone clasts that overlie coarse to fine sands and muds. Where currents are slower, the predominating substratum often consists of sandy muds. Species richness is usually greater on the gravelly substrata.

A small area of the river ($\sim 5 \times 15$ m) located ~ 16.5 km (river distance) from the mouth and ~ 0.6 km south of the end of Banks Road was selected for its remoteness from human disturbance and homogenous sedimentary bottom. This section has the gravelly bottom characteristic of large sections of the river and moreover, is about as rich in benthic macroinvertebrate species for any particular time of year as any other sampled area of the river (excluding riffles). During July-September 1975 the observed bottom water temperature in this area ranged from 23 to 27°C, water depth varied from 30 to 70 cm, and current velocity ranged from 4 to 18 cm/sec. Two successive recolonization experiments were subsequently performed at this site (Fig. 1.).

MATERIALS AND METHODS

The river was sampled in three ways. *Grab samples* were taken by inserting into the river bottom a plastic container open on one end. The container was placed open-end-downward and pushed vertically into the sediment until it was full. Then the surrounding sediment was dug away from the sides and bottom of the container, a cap was placed over the open end, and the

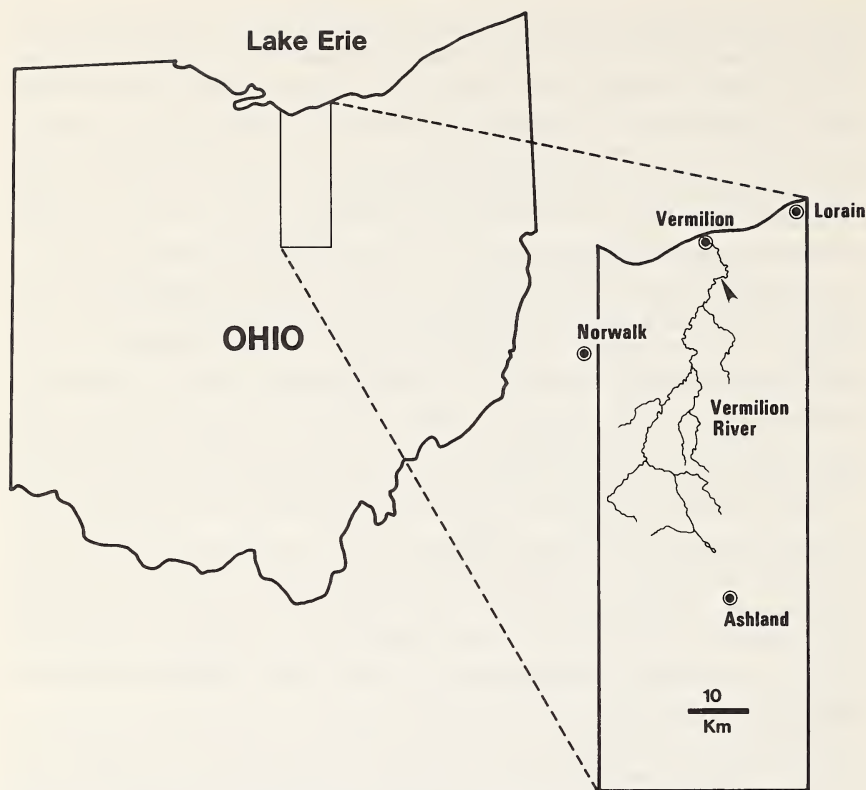


Fig. 1. Location of the Vermilion River, Ohio. Arrow indicates the study area.

container was removed from the sediment. The open end of the container measured 10 cm \times 10 cm, and its height was 14 cm. Thus each "grab" sampled about 100 cm² of bottom to a depth of 14 cm (slight flexing of the sides and bottom of the container during sampling make these figures close approximations).

Williams and Hynes (1974) show that numerous macroinvertebrates occur to depths of about 30 cm within the substrata of certain streams, with maximum organism densities occurring at 10 cm. Additionally they report a few species living at depths of up to 80 cm. Deep excavations into the substratum of the Vermilion River showed that in June-September 1975 most macroinvertebrates occurring in the study area were living in the upper 5-10 cm of the substratum. While oligochaetes were occasionally found below this level to depths of 20 cm or more, aquarium studies showed that they usually penetrated to this depth as an avoidance response to physical disturbance, and were not characteristically

living there. Since the grab samples penetrated to a depth of 14 cm, they were likely an adequate means of determining for the area they covered the abundance and taxonomic composition of most macroinvertebrate taxa excluding oligochaetes.

Recolonization samples were obtained by filling containers of the dimensions mentioned above with river sediments from the experiment site. These sediments had previously been dried, treated with boiling water, and dried again to remove all macroinvertebrates and their eggs and resting stages. The containers were capped and placed in the river in an area of substratum upstream from any previous sampling disturbance. The containers were sunk in the bottom until the lip was nearly flush with the river bed. By extending slightly above the substratum, the containers represented a small positive area on the bottom even when covered by subsequently deposited sediments. This facilitated locating the samples. The lids were then removed and the individual containers collected at predetermined intervals. Covers were placed on the containers just prior to sampling.

Removing, treating, and replanting the substratum obviously altered such properties as porosity, organic content, and probably grain size. Nevertheless, the gross physical aspects of the substratum remained the same as that of the river bed, save that it lacked macrofauna.

Rapid sedimentary accumulation (within 1-2 days) up to and over the edges of the containers meant that they were susceptible to recolonization from the four main recolonizing avenues employed by river organisms (upstream migration within the water, drift, within substratum migration, and oviposition [Williams and Hynes, 1976]).

Drift samples were obtained by attaching a net (7 threads/cm) with an opening of 32 cm to an iron support and placing it for 24 hours in the river with the open end facing upstream. The net was elevated approximately 4 cm off the bottom to exclude organisms crawling along the substratum.

Fouling of the drift net by sediments, leaves, and wood frequently occurred during the sampling interval and caused resistance to water flow through the net. This impedence to flow sometimes caused eddying near the mouth of the net, which may have lowered sampling efficiency. Thus the drift samples likely provide only a very rough estimate of the relative abundance of drifting organisms and may have excluded rare species. Although the net material consisted of 7 threads/cm, the material was fastened to the net in a double layer, and organisms less than $\frac{1}{2}$ mm in length were occasionally retained.

Approximately forty grab samples were taken in late June 1975 near the experimental sites to determine the taxonomic composition of the bottom in this section of the river. Analysis of these samples showed that over 90% of the

species sampled occurred in any given set of four samples. Also, the relative abundance of organisms in these four samples correspond to the relative abundance in all samples. So for the purposes of the experiment, the contents of four grab samples were considered representative of the fauna for this small area of river (see also Cain, 1938). Similarly, the contents of four simultaneously collected recolonization samples were considered representative of how this area would appear at a given instant of time after defaunation.

All benthic macroinvertebrates (\equiv size ≥ 1 mm) were picked by hand from all samples within 12 hours of collection. The organisms were preserved in 70% ethanol.

Two consecutive recolonization experiments were run in the following manner: For the first experiment, 20 recolonization sample "islands" were planted in the river bed on 2 July 1975. The original plan was to collect 4 boxes at a time, once a week, for 5 consecutive weeks. However, problems in locating the islands on the 3rd week of the experiment extended the experiment an extra week. The final set of 4 recolonization samples was collected on 13 August. The 4 recolonization samples were always selected at random. One drift sample was also taken simultaneously with each set of 4 recolonization samples. Experimentation with multiple drift samples revealed no noticeable differences in taxonomic composition or relative abundance of organisms among different samples. Two sets of 4 grab samples of the surrounding natural bottom were also taken during the course of the 5 week experiment.

A second experiment was initiated on 13 August when 32 defaunated sediment samples were planted in the river upstream and laterally displaced from the previous experiment site. Four recolonization samples were taken simultaneously every 3rd day. One drift sample was also taken at each sampling interval. Two sets of 4 grab samples were also taken during this time. The final set of 4 recolonization samples was collected on 6 September 1975.

RESULTS

The recolonization samples from both experiments (Tables 1, 2) show that the earliest colonizers were mostly immature Insecta. In the first experiment, all insect taxa found in the grab samples were present in the recolonization samples by the end of the first week (Tables 1, 3). In the second experiment, 4 of the 5 insect taxa found in the grab samples were also found in the recolonization samples taken 3 days after the beginning of the experiment (Tables 2, 4). Besides the immature insects, the gastropod *Oxytrema* was the only other taxon to colonize the samples during the first week. All these early colonizers were represented during the course of the experiments in the drift samples (see also Tables 5, 6).

TABLE 1
Description of Recolonization Samples for Experiment I

<i>Taxa</i>	<i>Sampling Week</i> (Samples taken at weekly intervals July 9 - August 13, 1975)					
	1	2	4**	5	6	
Arthropoda						
Insecta						
Diptera						
Chironomidae	18*	6*	17*	8*		14*
Coleoptera	2	0*	6	3*		0
Stenelminis						
Plecoptera	2	4*	8*	2*		1
Acroneuria						
Megaloptera						
Sialis	1*	1	4	0		1
Ephemeroptera						
Hexagenia	2*	8	8	2		8
Annelida						
Oligochaeta	0	0	12	3		1
Mollusca						
Gastropoda						
Oxytrema	1	0*	2	0		0
Bivalvia						
Sphaerium	0	0	0	1		2

key: * = Present in drift samples taken simultaneously.
 ** = No samples collected during week 3 of experiment.
All Insecta represented as aquatic immatures.
Organism numbers = #individuals/400 cm²

TABLE 2

Description of Recolonization Samples for Experiment II

Taxa	Sampling Period							
	(Samples taken every third day beginning Aug. 16—ending Sept. 6, 1975)							
	1	2	3	4	5	6	7	8
Arthropoda								
Insecta								
Diptera								
Chironomidae								
Coleoptera	21*	35*	51*	28	9	14	9	21
Stenelmis	1	0	0	0	0*	0	0	3
Ephemeroptera	0	0	0	1*	0*	2*	1	0
Ephemera	1*	3	1	0*	0	0*	0*	0
Heptageniidae	3*	8*	4	8*	20*	20	1*	6*
Caenidae								
Annelida								
Oligochaeta								2
Mollusca								
Gastropoda								
Oxytrema	0	1*	4*	0*	3	4*	1	1
Ferrissia								2
Bivalvia								
Sphaerium							1	1
Lasmigona								2

Key: * denotes taxa also found in corresponding drift sample.
 Organism numbers = #individuals/400 cm²

TABLE 3
Description of Grab Samples for Experiment I

Taxa	Sampling Week	
	1	2
Arthropoda		
Insecta		
Diptera		
Chironomidae	18	19
Coleoptera		
<i>Stenelmis</i>	5	3
Plecoptera		
<i>Acroneuria</i>	8	2
Megaloptera		
<i>Sialis</i>	0	2
Ephemeroptera		
<i>Ephemera</i>	8	9
Annelida		
Oligochaeta	3	4
Mollusca		
Gastropoda		
<i>Oxytrema</i>	1	1
<i>Ferrissia</i>	0	1
Bivalvia		
<i>Sphaerium</i>	1	1

All Insecta represented as aquatic immatures.

Organism numbers = # individuals/400cm²

The last organisms to appear in the recolonization samples were oligochaetes, bivalves, and the gastropod *Ferrissia*. In the first experiment, oligochaetes colonized the samples during the interval between the 2nd and 4th week, and bivalves appeared by the 5th week. In the second experiment, the oligochaetes and *Ferrissia* appeared between the sampling times of the 21st and 24th days. None of these organisms ever occurred in the drift samples. Although all taxa from the grab samples eventually appeared in the recolonization samples, these 2 kinds of samples were never identical taxonomically for any sampling period. Nevertheless, recolonization samples always grew biologically to resemble most closely the grab samples instead of the drift samples, and organisms that occurred abundantly in drift samples were sometimes uncommon or absent entirely from the recolonization samples (Compare Tables 1, 2, to Tables 5, 6).

The pattern of colonization with respect to the overall abundance of organisms was marked by large fluctuations (Figs. 2, 3). Both for the abundance pattern as a whole and with respect to any particular taxon, there were no

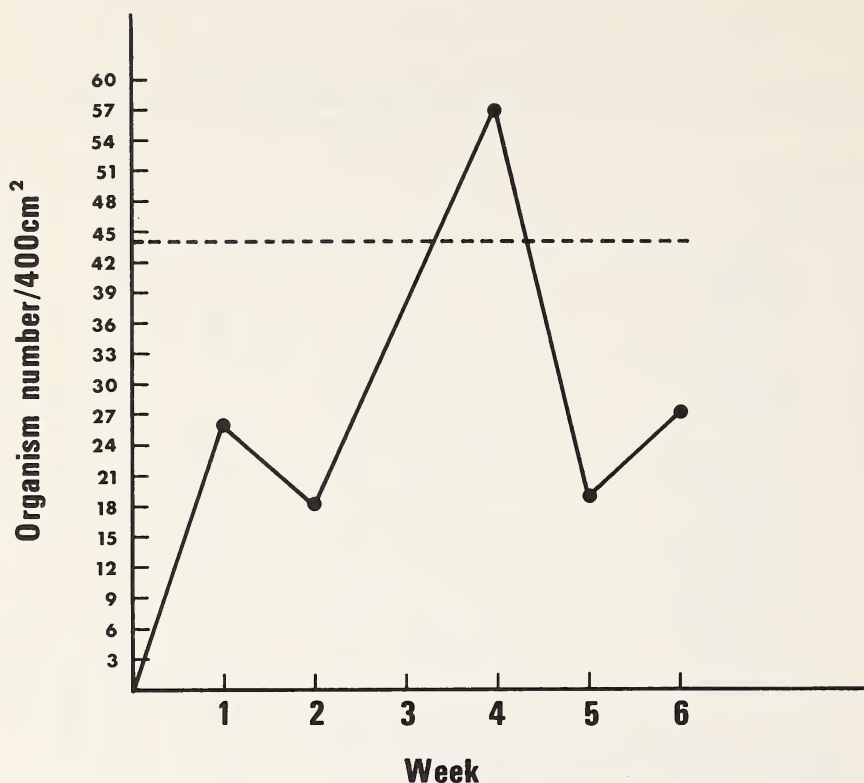


Fig. 2. Organism abundance fluctuations for the first experiment. The dashed line represents the summation of the average number of individuals per taxon collected from the grab samples.

long, uniform trends. Also, peak abundances were often reached, for each taxon and collectively, prior to the last sampling interval.

Although not all sampled organisms were measured, a qualitative assessment of their size patterns showed that this often varied widely for particular taxa within each sample and among samples taken at different times. Hence there was no discernable pattern of organism size (or age) with respect to the sequence of recolonization.

DISCUSSION

One of the main distinctions between the early and late recolonizers is that the early recolonizers are drift-prone and the later recolonizers are not. Thus drift is likely an important mechanism in the early recolonization process in the

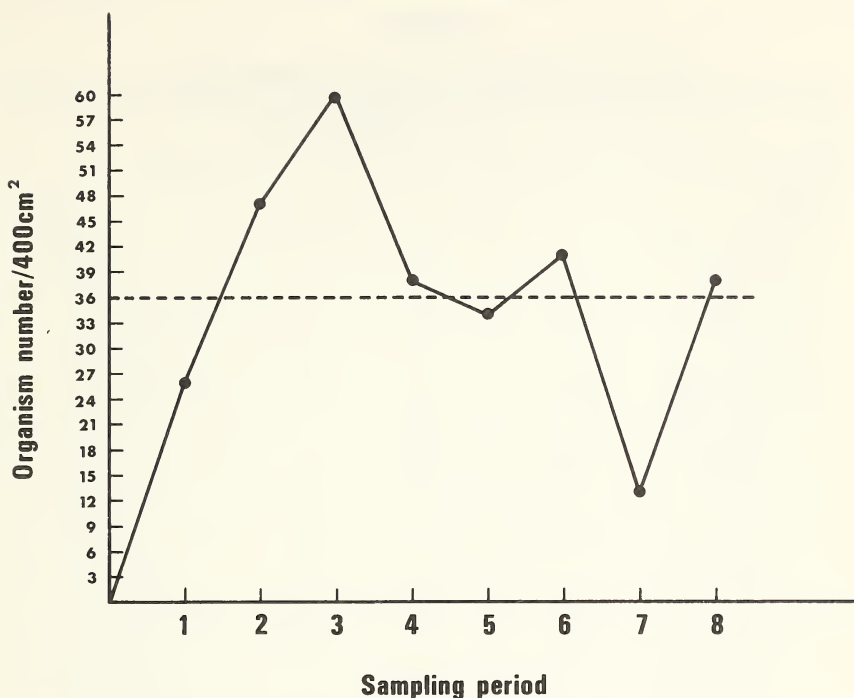


Fig. 3. Organism abundance fluctuations for the second experiment. The dashed line represents the summation of the average number of individuals per taxon collected from the grab samples.

Vermilion River. This inference is supported by Waters (1964), who shows drift to be responsible for rapid recolonization by *Baetis vagans* (mayfly) and *Gammarus limnaeus* (amphipod) in Valley Creek, Minnesota.

Nevertheless, as noted previously, the recolonization samples always more closely resembled the taxonomic composition of the grab, rather than the drift samples. This indicates that while drift is important in the early recolonizing process in this river, drift-aided recolonization is not a haphazard process dictated by the total composition of the drift fauna. Moreover, it suggests that particular organisms have an ability to select particular sites at which they may terminate drifting.

Of the other possible sources of recolonizing organisms, oviposition was likely not a major source for the Vermilion River during this time of year. Inspection of the recolonization samples showed that while the colonizing organisms varied widely intraspecifically in size, they were generally larger than they would have been had they hatched from eggs at any time during the experiment.

TABLE 4
Description of Grab Samples for Experiment II

Taxa	Sampling period	
Arthropoda	1	4
Insecta		
Diptera		
Chironomidae	25	17
Coleoptera		
<i>Stenelmis</i>	4	3
Megaloptera		
<i>Sialis</i>	1	0
Ephemeroptera		
<i>Ephemera</i>	1	0
Heptageniidae	1	1
Caenidae	5	2
Annelida		
<i>Oligochaeta</i>	4	2
Mollusca		
Gastropoda		
<i>Ferrissia</i>	1	1
<i>Oxytrema</i>	1	3
Bivalvia		
<i>Sphaerium</i>	1	1
<i>Lasmigona</i>	0	1

All Insecta represented as aquatic immatures.

Organism numbers = # individuals/400cm²

By process of elimination, the absence of oligochaetes, bivalves, and the gastropod *Ferrissia* from the drift samples indicates these organisms colonized the experimental islands by migration within the substratum or by upstream migration within the water.

Some of the early recolonizers are also more abundant on the undisturbed river bottom than are the later recolonizers (Tables 3, 4). This suggests that the higher the relative abundance of a particular taxon, the greater the chance of its being a successful early recolonizer. Thus it is entirely conceivable that highly mobile but nondrifting organisms (e.g., *Sphaerium*, *Oligochaeta*) may have appeared on the islands earlier had these taxa been more abundant.

In the sense of having 1) all taxa in the grab samples represented at some time on the islands, and 2) total organism number in the grab samples at least equaled on the islands, recolonization was complete for both experiments by the 5th week and 24th day, respectively. Although exact equivalence in taxonomic richness and organism number was not achieved between the grab

TABLE 5
Description of Drift Samples for Experiment I

Taxa	Sampling week				
	1	2	4*	5	6
Arthropoda					
Insecta					
Diptera					
Chironomidae	A	A	A	A	A
Coleoptera					
<i>Psephenus</i>	C				
<i>Stenelmis (a)</i>	A		R	C	C
<i>Stenelmis</i>		C		R	
Plecoptera					
<i>Acroneuria</i>		C	R	C	
Megaloptera					
<i>Sialis</i>	R				
Ephemeroptera					
<i>Ephemer</i>	A				
<i>Callibaetis</i>	A	C	C	R	C
Heptageniidae	C				
Caenidae	C		C	R	
Trichoptera					
<i>Hydropsyche</i>	C	C			
<i>Chimarra</i>	R				
Odonata					
<i>Clithemis</i>					R
Heteroptera	C				
Corixidae					
Mollusca					
Gastropoda					
<i>Oxytrema</i>		R			
<i>Physa</i>	R				

Key: *No samples collected during week 3 of experiment

A = Abundant > 10 individuals

C = Common = 2–9 individuals

R = 1 individual

All Insecta represented are immatures unless denoted by “(a)” signifying adult.

samples and islands by the end of the experiment, the discrepancy could possibly be attributed to one or both of the following causes: 1) differences between the microenvironments of the islands and area where the grab samples were taken, and 2) unequal biotic modification of the different areas by the numerous observed storm events. These possible causes, plus the additional

TABLE 6
Description of Drift Samples for Experiment II

Taxa	Sampling period							
	(Samples taken every third day beginning Aug. 16—ending Sept. 6, 1975)							
	1	2	3	4	5	6	7	8
Arthropoda								
Insecta								
Diptera								
Chironomidae	A	A	A	A	A	A	A	A
Coleoptera								
<i>Stenelmis</i> (a)	R	R	R	C				
<i>Stenelmis</i>					R			
Plecoptera								
<i>Acroneuria</i>	R					R		
Ephemeroptera								
<i>Ephemera</i>				R	R	R		
<i>Callibaetis</i>	A			A		R	R	
Heptageniidae	A		R	A	C		R	
Caenidae	C	C		C	C		C	R
Trichoptera								
<i>Hydropsyche</i>				R				
Odonata								
<i>Clithemis</i>								R
Heteroptera								
Corixidae				C				
Mollusca								
Gastropoda								
<i>Oxytrema</i>	C	C	C			R		

Key: A = Abundant > 10 individuals
C = Common = 2–9 individuals
R = Rare = 1 individual

All Insecta represented are immatures unless denoted by “(a)” signifying adult.

factors of emergence of adult insects and possible population density regulation through drift (Waters, 1966; Dimond, 1967), might also explain the pronounced fluctuations in organism number during both experiments.

The time scale involved in the recolonization of this area of the Vermilion River is roughly similar to the findings of other workers for different streams. For example, Waters (1964) finds 1–2 days sometimes a sufficient recolonizing time for numerically dominant invertebrates in a Minnesota stream. Mason et al. (1967) suggest “about six weeks” is an adequate time for recolonization by

rock-adhering or rock-clinging invertebrates in large streams. Williams and Hynes (1976) drawing upon previously published sources, believe 28 days to be a reasonable average time for their field area in Ontario.

For the Vermilion River, this all suggests that the benthic macroinvertebrate population may rapidly recover from a local disaster if there are 1) no permanent, major, physical and chemical alterations in the environment, and 2) if there are organisms available nearby in the river to repopulate the affected area. For rivers in general, the overall kind, extent, and duration of the disaster can greatly increase this recovery time (Cairns et al. 1971).

Colonization studies that are precisely comparable to the present one are lacking for lentic environments. This is because most lentic colonization studies performed to date involve a situation in which the environment is extensively physically modified by abiotic factors prior to the completion of colonization (e.g., as in the filling of an impoundment or a dry lake; see Paterson and Fernando, 1969; McLachlan, 1975). These physical changes, such as modification of water depth and a change from a lotic to lentic system, are time consuming and may help retard the completion of colonization by a year or more.

For the marine realm, the experiments performed by McCall (1977) are not only comparable to the present study, but also provide notably contrasting results. McCall showed for Long Island Sound that most early colonizers settle from the water column onto defaunated bottom as larvae or very young juveniles. Mobility subsequent to settling is restricted. An easily recognizable succession occurs wherein opportunistic, or "r"-strategist, species initially colonize the area, only to be replaced later by more diverse assemblages of "K"-strategist species. The time for complete recolonization is approximately one year.

In the Vermilion River, recolonization takes place by either immature stages of varying age or by adults. Thus the colonization process is more of a function of relative mobility (drift, bottom migration) and relative abundance on the natural bottom and is not mainly a reproductive event. Also, no obvious pattern of succession could be identified for the Vermilion River, and the time involved in complete recolonization was much less than that for Long Island Sound.

This rapid recolonizing ability of lotic benthos is highly adaptive to the extremely rigorous physical nature of their habitat. Removal of organisms from areas of river bottom is likely a continual but spatially patchy phenomenon caused by such factors as floods, ice scour, and sediment transport. The ability of organisms to quickly recolonize areas following natural defaunation helps insure maximal dispersal within their habitat. This ability would help promote

the maintenance of high population levels within the habitat by reducing the potential for intraspecific competition. Also, wide dispersal would mean that as local populations are wiped out by changing environmental conditions, undisturbed populations of organisms are present elsewhere in the river to help insure the species' survival.

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A NEW SPECIES OF THE GENUS *AUSTRALOPITHECUS* (PRIMATES: HOMINIDAE) FROM THE PLIOCENE OF EASTERN AFRICA

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ABSTRACT

Hominid fossils have recently been recovered from Pliocene age deposits at Hadar, Ethiopia, and Laetolil, Tanzania. These fossils share an array of distinctive morphological characteristics which suggests that they belong to a single species of the genus *Australopithecus*, differing significantly from those previously described. The binomen *Australopithecus afarensis* sp. nov. is therefore assigned to this collection of early hominid remains.

A substantial collection of hominid fossils has recently been recovered from two Pliocene sites in eastern Africa. Hominid specimens from Hadar in Ethiopia (11°N, 40°30'E) and Laetolil in Tanzania (3°12'S, 35°11'E) have been dated to between ca. 2.9 and ca. 3.7 million years before present (Aronson et al., 1977; Leakey et al., 1977). The strong morphological continuity between these two samples suggests that they are best considered as representing a single taxon; hence, the Hadar and Laetolil fossils currently constitute the oldest indisputable evidence of the family Hominidae.

Some of these specimens have been provisionally allocated to *Homo* sp. indet. (Johanson and Taieb, 1976; Leakey et al., 1977) while others have been referred to *Australopithecus* aff. *africanus* (Johanson and Taieb, 1976). Subsequent to this preliminary assessment, more detailed study of the entire hominid sample from Laetolil and Hadar has provided us with new information indicating that 1) the specimens belong to only a single taxon, and 2) they differ significantly from previously recognized species of Plio/Pleistocene Hominidae. The Hadar and Laetolil hominids exhibit many morphological features found in specimens attributed to the genus *Australopithecus* (*sensu lato*) (as defined by Le Gros Clark, 1955) and they are therefore assigned to this taxon. Careful evaluation of the material has led to the recognition of a distinctive suite of morphological traits distinguishing the Laetolil and Hadar remains from other hominid taxa. Such study indicates the necessity of assigning these fossils to a new and more primitive species of *Australopithecus*.

Order PRIMATES Linnaeus 1758

Superfamily HOMINOIDEA Simpson 1931

Family HOMINIDAE (Le Gros Clark 1955)

Genus *Australopithecus* Dart 1925

Australopithecus afarensis sp. nov.

Synonymy:

1950 *Meganthropus africanus* Weinert, H.: 139

1955 *Praeanthropus africanus* Şenyürek, M.: 33

Holotype:

Laetolil Hominid (L.H.-) 4, mandibular corpus with broken RC, M₁, M₂; intact R and LP₄; RP₃, M₃; LM₁, M₂.

Locality:

Locality 7 of the Laetolil Site, Tanzania, collected in 1974 by M. Muluila.

Horizon:

Laetolil Beds between Aeolian Tuffs b and c, Pliocene age (3.6–3.7 m.y. b.p.)

Paratypes:

Laetolil Beds, Tanzania:

L.H.-1, RP⁴; L.H.-2, immature mandibular corpus with permanent and deciduous teeth; L.H.-3(a-t), isolated upper and lower deciduous and permanent teeth; L.H.-3/6a, b, Rdc-, Ldm¹; L.H.-5, R. maxillary row, I²-M¹; L.H.-6(a-e), isolated permanent and deciduous upper teeth; L.H.-7, RM⁻ frag.; L.H.-8, RM², RM³; L.H.-10, L. edentulous mandibular frag.; L.H.-11, LM^{1/2}; L.H.-12, LM^{2/3} frag.; L.H.-13, R. edentulous mandibular corpus frag.; L.H.-14(a-h), isolated lower teeth; Garusi maxilla, RP³-P⁴.

Hadar Formation, Ethiopia:

Sidi Hakoma Member:

A.L. 128-1, L. prox. femur frag.; A.L. 128-23, R. mandibular corpus, C-M₂; A.L. 129-1a, b, c, femur and tibia frags.; A.L. 129-52, L. ischium; A.L. 137-48a, R. distal humerus; A.L. 137-48b, R. distal ulna; A.L. 145-35, L. mandibular corpus, P₃-M₂; A.L. 166-9, L. temporal frag.; A.L. 198-1, L. mandibular corpus, C-M₃; A.L. 198-17a, b, LI¹, LI²; A.L. 198-18, RI₂; A.L. 199-1, R. maxilla, C-M³; A.L. 200-1a, maxilla, complete dentition; A.L. 200-1b, RM₁; A.L. 211-1, R. prox. femur frag.; A.L. 228-1, R. diaphysis femur; A.L. 266-1, mandibular corpus, LP₃-M₁, RP₃-M₃; A.L. 277-1, L. mandibular corpus, C-M₂; A.L. 311-1, L. mandibular corpus, P₃; A.L. 322-1, L. distal humerus; A.L. 400-1a, mandibular corpus, LI₁-M₃, RI₂-M₃; A.L. 400-1b, RC⁻; A.L. 411-1, R. mandibular corpus, M₁-M₃.

Denan Dora Member:

A.L. 161-40, LM³; A.L. 188-1, R. mandibular corpus, M₂-M₃; A.L. 207-13, L. mandibular corpus, P₃-M₂; A.L. 241-14, LM⁻; A.L. 366-1, LM₃; A.L. 388-1, LM³.

A.L. 333-1, facial frag. and maxilla, RP^3 - P^4 , LC - P^3 ; -2, maxilla, RC - M^1 , LI^2 - P^4 ; -3, R. prox. femur; -4, R. distal femur; -5, L. prox. tibia frag.; -6, L. distal tibia; -7, L. distal tibia; -8, R. calcaneum frag.; -9a, -9b, R. and L. distal fibulae; -10, L. mandibular corpus frag., P^3 ; -11, R. prox. ulna frag.; -12, R. distal ulna; -13, L. prox. V metatarsal (MT); -14, R. V metacarpal (MC); -15, L. prox. II MC; -16, L. III MC; -17, R. distal V MC; -18, R. distal IV MC; -19, prox. hand phalanx; -20, prox. hand phalanx frag.; -21, distal MT; -22, prox. hand phalanx frag.; -23, cranial frag.; -25, intermed. hand phalanx; -26, prox. phalanx; -27, R. distal II MC; -28, R. medial cuneiform frag.; -29, L. distal humerus; -30, Rdm_1 ; -31, prox. hand phalanx frag.; -32, intermed. hand phalanx; -33, prox. hand phalanx; -34, immature metapodial; -35, Rdc_- ; -36, R. foot navicular; -37, R. calcaneum frag.; -38, L. immature distal ulna; -39, L. immature prox. tibia; -40, R. capitate; -41, R. med. femoral condyle frag.; -42, L. prox. tibia; -43a, b, L. and R. mandibular corpi, R. and L. dm_1 - dm_2 ; -44, LM^- ; -45, partial cranium; -46, intermed. hand phalanx; -47, R. foot navicular; -48, L. II MC; -49, prox. hand phalanx frag.; -50, R. hamate; -51, body thoracic vertebra; -52, frag. M_- ; -53, thoracic vertebra frag.; -54, L. prox. I MT; -55, L. calcaneum frag.; -56, L. IV MC; -57, prox. hand phalanx; -58, R. prox. I MC frag.; -59, R. mandibular corpus frag., M_2 - M_3 ; -60, prox. phalanx; -61, L. distal femur frag.; -62, prox. hand phalanx; -63, prox. hand phalanx; -64, intermed. hand phalanx; -65, R. prox. III MC; -66, Ldc^- ; -67, Rdi^2 ; -68, Ldi_2 ; -69, L. prox. hand phalanx; -70, immature metapodial; -71, prox. foot phalanx; -72, MT frag.; -73, body lumbar vertebra; -74, L. mandibular corpus frag., M_1 - M_3 ; -75, head R. talus; -76, Ldi_2 ; -77, Ldc_- ; -78, L. prox. V MT; -79, L. lateral cuneiform; -80, R. trapezium; -81, body immature thoracic vertebra; -82 LI^1 ; -83 atlas vertebra frag.; -84, R. temporal frag; -85, L. distal fibula; -86, maxilla, L. and R. dm^1 - dm^2 , M^1 ; -87, L. prox. humerus frag.; -88, intermed. hand phalanx; -89, L. V MC; -90, LC_- ; -92, immature long bone frag.; -93, prox. hand phalanx; -94, L. clavicle frag.; -95, R. prox. femur; -96, L. distal tibia; -97, L. mandibular corpus frag.; -98, R. prox. radius; -99, Ldc^- ; -100, L. coronoid process mandible; -101, axis vertebra; -102, prox. hand phalanx; -103, RC_- ; -104, Rdc^- ; -105, partial immature cranium, Rdm^1 - dm^2 ;

-106, cervical vertebra; -107, R. prox. humerus; -108, L. ascending ramus; -109, humerus shaft frag.; -110, L. immature distal femur frag.; -111, R. immature distal femur frag.; -113, immature long bone frag.; -115, associated foot bones.

A.L. 333w-la-e, R. and L. mandibular corpi, LP₃-M₂, RP₃-M₂, RM₃ frag., R. condyle; -2, LC⁻; -3, LI₂; -4, prox. hand phalanx; -5, R. distal II MC; -6, R. prox. III MC; -7, immature prox. hand phalanx; -8, vertebra frag.; -9a, b, LI₁, LI₂; -10, RC₋; -11, distal hand phalanx; -12, R. mandibular corpus frag., M₁; -13, prox. fibula; -15, R. coronoid process mandible; -16, L. mandibular condyle; -17, -18, -19, rib frags.; -20, immature prox. hand phalanx frag.; -21, immature phalanx; -22 R. distal humerus frag.; -23, R. immature II MC; -25, prox. hand phalanx frag.; -26, L. prox. V MC; -27, L. mandibular corpus, M₂; -28, RI²; -29, immature prox. phalanx frag.; -30, rib; -31, L. distal humerus frag.; -32, R. mandibular corpus, M₃; -33, R. prox. radius; -34, intermed. hand phalanx frag.; -35, L. prox. V MC; -36, L. prox. ulna; -37, L. distal fibula -38, intermed. hand phalanx; -39, R. I MC; -40, R. prox. femur frag.; -41, rib frag.; -42, RP⁴; -43, immature prox. IMT frag.; -45, rib frag.; -46, R. mandibular corpus, P₃; -47, rib frag.; -48, RM₂; -50, distal hand phalanx; -51, prox. hand phalanx frag.; -52, L. mandibular condyle; -53, intermed. hand phalanx frag.; -54, prox. hand phalanx frag.; -55, MT frag.; -56, R. distal femur; -57, L. mandibular corpus, M₂-M₃; -58, mandibular corpus frag., LI₁-P₄, RI₁-C₋; -59, L. mandibular corpus, M₂-M₃; -60, mandibular corpus, LP₃-M₃, RI₁-C₋.

A.L. 333x-1, RM³; -2, LI²; -3, LC⁻; -4, RI¹; -5, R. prox. ulna; -6, -9, R. clavicle frags.; -12, thoracic vertebra; -13a, prox. hand phalanx; -13b, intermed. hand phalanx; -14, -15, prox. radial epiphyses; -17, RI²; -18, intermed. hand phalanx; -20, RI¹; -21a, b, intermed. hand phalanges; -25, di_{1/2}; -26, R. prox. tibia.

Kada Hadar Member:

A. L. 288-1, partial skeleton.

Horizon:

Laetoli Beds, Tanzania. Known hominid sample from between strata dated to 3.59 and 3.77 m.y.

Hadar Formation, Ethiopia. Sidi Hakoma Member dated to older than ca. 3.0 m.y., but less than ca. 3.3 m.y. Denan Dora and Kada Hadar Members dated to younger than ca. 3.0 and older than ca. 2.6 m.y. with the latter member stratigraphically above the former.

Diagnosis:

A species of *Australopithecus* distinguished by the following characters:

Dentition

Upper central incisors relatively and absolutely large; upper central and diminutive lateral incisors with strong lingual basal tubercles, upper incisors with flexed roots; strong variation in canine size, canines asymmetric, lowers with strong lingual ridge, uppers usually with exposed dentine strip along distal edge when worn; P_3 occlusal outline elongate oval in shape with main axis mesiobuccal to distolingual at 45° – 60° to tooth row, dominant mesiodistally-elongate buccal cusp, small lingual cusp often expressed only as inflated lingual ridge; diastemata often present between I^2/C^- and C_-/P_3 ; C^-/P_3 complex not functionally analogous to pongid condition.

Mandible

Ascending ramus broad, not high; corpus of larger specimens relatively deep anteriorly and hollowed in region of low mental foramen which usually opens anterosuperiorly; moderate superior transverse torus; low rounded inferior transverse torus; anterior corpus rounded and bulbous; strong posterior angulation of symphyseal axis; postcanine teeth aligned in straight rows; arcade tends to be sub-rectangular, smaller mandibles with relatively narrow incisor region.

Cranium

Strong alveolar prognathism with convex clivus; palate shallow, especially anteriorly; dental arcade long, narrow, straight sided; facial skeleton exhibiting large, pillar-like canine juga separated from zygomatic processes by deep hollows, large zygomatic processes located above P^4/M^1 and oriented at right angles to tooth row with inferior margins flared anteriorly and laterally; occipital region characterized by compound temporal/nuchal crest (in larger specimens), concave nuchal plane short anteroposteriorly; large, flattened mastoids; shallow mandibular fossae with weak articular eminences placed only partly under braincase; occipital condyles with strong ventral angulation.

Postcranium

See remarks.

Description:

Dentition

Large canines project beyond tooth rows and possess massive, long roots; buccal face of P_3 's often with vertical wear striae caused by occlusion with upper canines; P_3 's often with two distinct roots, the mesial one round and angulated mesio-buccally, the distal one plate-like and oriented transverse to the tooth row; P^3 's sometimes three rooted, with pointed buccal cusp, extensive and asymmetric buccal face, buccal cervicoenamel line projecting towards mesio-buccal root, and the lingual cusp situated mesial to buccal cusp, P^3 's tend to be larger than P^{4*} 's and the latter do not show mesiodistal elongation of the buccal crown half; lower molars, especially M_1 and M_2 tend to be square with cusps arranged in Y-5 pattern; wide occlusal foveae on all molars; strong molar size gradient of $M_3 > M_2 > M_1$; hypocones and hypoconulids large; deciduous canines similar to the permanent ones in form and occlusal projection; dm_1 's molarized, with linguallly facing anterior foveae and deep buccal grooves; substantial variation in tooth size.

Mandible

Ascending ramus slopes posteriorly and joins corpus at high position defining narrow extramolar sulcus; broad condyles; mandibular canal immediately below distal M_3 root; base of corpus everted.

Cranium

Incisors procumbent; lower margin of pyriform aperture marked laterally by raised borders; tooth rows tend to converge posteriorly; strong muscle markings on vault and cranial base, temporal lines converge anteriorly, but presence of sagittal cresting unknown; lateral portion of cranial base highly pneumatized; occipital condyles placed below external auditory meatus in lateral view; estimated cranial capacity small relative to *Homo* sp.; broad mandibular fossae, laterally projecting postglenoid process; pyramid process angles anteriorly relative to more transverse tympanic plate.

Postcranium

Strong dimorphism in body size; all skeletal elements with high

level of robusticity in muscle and tendon insertions; pelvic region and lower limbs indicate adaptation to bipedal locomotion; "waisted" appearance of capitate; third metacarpal lacking styloid process; phalanges strongly longitudinally curved; foot navicular with cuboideonavicular facet; deep peroneal grooves on distal fibulae; anterior margin of ilium between anterior superior and inferior spines relatively straight; cervical vertebrae with long spinous process; relatively high humerofemoral index compared to modern humans.

Etymology:

The species name *afarensis* derives from the Afar depression of northeastern Ethiopia, where the largest portion of the paratype series was recovered.

REMARKS

Laetolil Hominid-4 was selected as the holotype both because of its distinctive, diagnostic morphology and because it has previously been fully described and illustrated (White, 1977). The generic name *Praeanthropus* originally proposed by Hennig (1948) is invalid because no species designation was given. Şenyürek (1955) used the generic nomen *Praeanthropus* and utilized Weinert's (1950) specific name *africanus*, designating the original Garusi maxillary fragment as *Praeanthropus africanus*. The present authors do not consider the original Garusi maxillary fragment or the new Laetolil and Hadar material to represent a hominid genus distinct from *Australopithecus*.

The authors recognize that individual traits and even single specimens in the new collections can be matched in other samples representing different taxa (e.g., *Australopithecus africanus* Dart 1925, *Homo habilis* Leakey, Tobias and Napier 1964). However, the overall character complex seen in the Hadar and Laetolil fossils is distinct from other previously found and described species. Care has been taken in the diagnosis to follow Mayr's suggestion to "list the most important characters or character combinations that are peculiar to the given taxon and by which it can be differentiated from other similar or closely related ones" (1969: p. 266). In the description of *Australopithecus afarensis* we have chosen to present a characterization of the entire hypodigm. This should insure that the presentation not be viewed as typological and should also given some indication of the variation recognized in this new taxon.

It is important to recognize that certain traits or complexes were not considered in the diagnosis but placed in the description due to the lack of comparable anatomical specimens from other species of *Australopithecus*.

Some of the traits, such as the morphology of the hand and foot bones, may be diagnostic of the new species, but this cannot be ascertained until pertinent new material is recovered from other sites.

The Hadar and Laetolil fossils appear to represent a distinctive early hominid form characterized by substantial size variation which is interpreted as reflecting sexual dimorphism. Members of this new taxon display a complex of primitive dental, cranial, and possibly postcranial characteristics. Recognition of the new species *Australopithecus afarensis* has important implications for interpretations of early hominid phylogeny. These implications will be considered in forthcoming publications.

ACKNOWLEDGMENTS

Fieldwork at Hadar and Laetolil was undertaken with the kind permission and cooperation of the Provisional Military Government of Socialist Ethiopia and the United Republic of Tanzania respectively. We thank the following institutions for financial support: the National Geographic Society, the National Science Foundation, the L. S. B. Leakey Foundation, the Wenner-Gren Foundation, the Cleveland Museum of Natural History, the Centre National de la Recherche Scientifique, and the Singer-Polignac Foundation.

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Appreciation is expressed to Dr. Maurice Taieb for his role in the discovery of Hadar and for his initiation and successful development of the International Afar Research Expedition. Special thanks are extended to Professor Ernst Mayr for critically reviewing the manuscript.



Fig. 1. Map of eastern Africa showing the locations of Hadar and Laetolil.



Fig. 2. Type specimen of the new species *Australopithecus afarensis*, the mandible L.H.-4 from Laetolil, Tanzania. Occlusal view. Natural size.



Fig. 3. Two distal femora from Hadar, Ethiopia (A.L. 333-4, left; A.L. 129-1a, right) indicating the size variation within the new species. Anterior view.

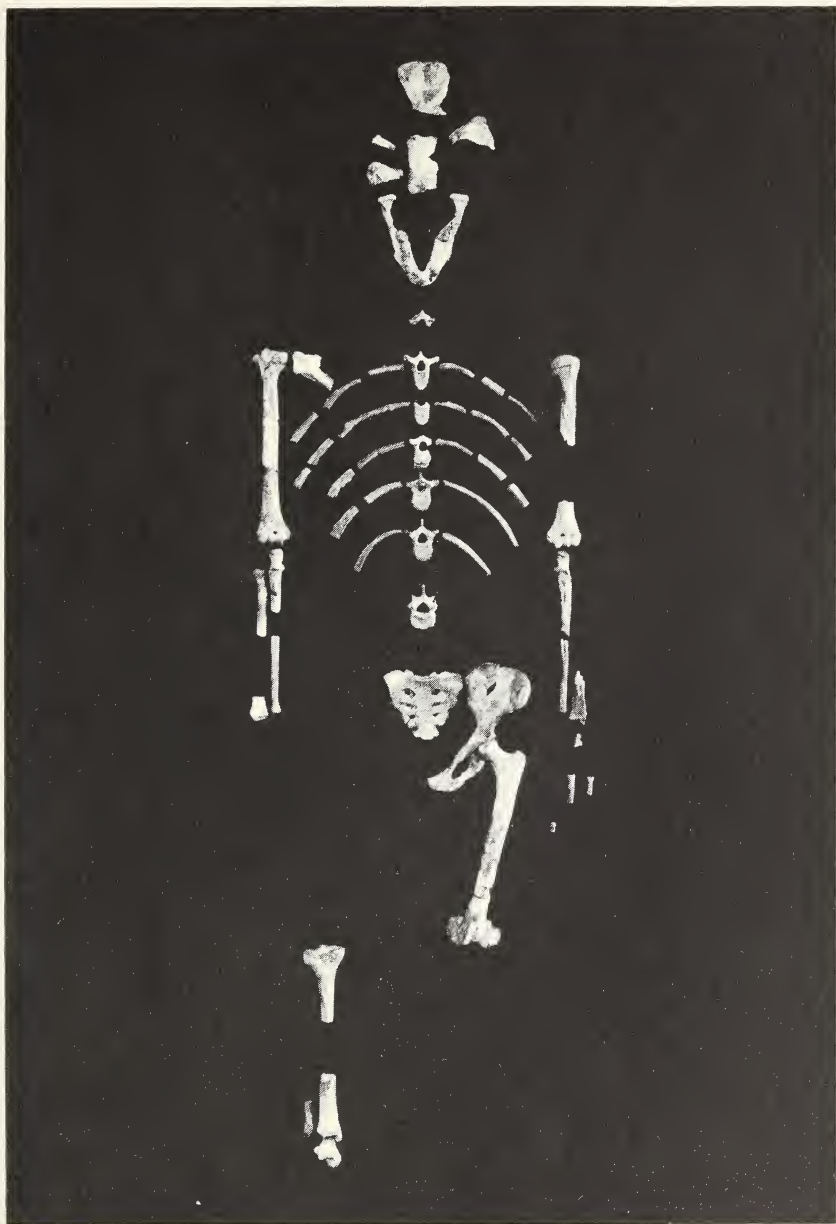


Fig. 4. The partial skeleton from Hadar, Ethiopia A.L. 288-1. The total length of the left femur is approximately 280 mm.

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PLIOCENE-PLEISTOCENE SUIDAE FROM HADAR, ETHIOPIA

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ABSTRACT

Three different suids occur in the Hadar Formation. *Nyanzachoerus pattersoni* is plentiful in the Sidi Hakoma member, especially in the lower part, and morphologically matches the type material from Kanapoi very closely. *Notochoerus euilus* ranges throughout, making up 61% of the total sample. The skull architecture is described for the first time. A small suid occurring throughout is regarded as a new species of *Kolpochoerus*, *K. afarensis*, distinguished from *K. limnetes* by its smaller size, simpler molars and more *Sus*-like features of the premolars. It is, in all probability, ancestral to *K. limnetes*. Comparison of the *Notochoerus euilus* material with that from the Usno Formation and the lower part of the Shungura Formation suggest that the lower Sidi Hakoma member may be in the range of 3.0 to 3.5 million years old.

INTRODUCTION

Addis Ababa, the capital of Ethiopia, lies in the center of the country at an elevation of 2,355 metres above sea level, not far from the source of the Awash river. This river drains northeastward into the Afar province, but derives much of its water from the highlands near the source area and from seasonal streams that flow into it from the western flanks of the Afar triangle. One of these streams, Kada Hadar, meets the Awash in an area that has yielded substantial amounts of fossil material, including important hominid remains (Taieb et al., 1972; Taieb, Johanson and Coppens, 1975). The broad framework of the geology has been considered by Taieb (1974) and the particular succession

exposed in the Hadar area has been described recently (Taieb et al., 1976), together with a preliminary account of the fossil remains and hominid discoveries (Johanson and Taieb, 1976). The Awash at Hadar is close to 500 m above sea level, with local relief of some 100 m and badland type dissection.

The Hadar Formation has a thickness of about 180-200 m, although the base of the lowest unit is not yet firmly established. The sediments are largely arenaceous and argillaceous and represent various phases in a fluctuating complex of lacustrine, lake margin and fluvial deposits, apparently related to a Pliocene-Pleistocene lake that occupied much of the Afar basin. Several minor erosional unconformities can be seen, but they do not appear to represent major breaks. A few steep normal faults, with displacements of 5 to 40 m occur. The Hadar Formation is capped unconformably by an unnamed unit of Pleistocene gravels and sands that contain hand axes.

The Hadar Formation has been divided into four members, conveniently separated by volcanic tuff horizons that are laterally extensive and usually altered to a chalky white material, forming useful "markers." The lowest tuff complex (SHT) divides the Basal Member (BM) from the Sidi Hakoma Member (SH) and in places it has been preserved in channels, where the material is not altered and consists largely of fresh glass shards. The Sidi Hakoma Member has been subdivided into four submembers (SH-1, SH-2, SH-3, SH-4) and within the upper submember there is at the eastern end of the Hadar area a magnetically reversed basalt flow, 1 to 4 m thick, that dies out towards the northwest. Its resistance to erosion resulted in the development of a minor plateau in this area, capped directly by the Pleistocene gravels. Preliminary K/Ar determinations on the basalt give ages of 2.9 ± 0.2 m.y. and 3.0 ± 0.2 m.y. (Aronson et al., 1977). The TT marker lies 20 m above the basalt level and is a very persistent zone of thin tuffs defining the base of the Denen Dora Member (DD); within this member, three submembers are recognised (DD-1, DD-2, DD-3). The KHT tuff is a single deposit that is laterally less extensive than the older tuffs but serves to define the base of the fourth member, the Kada Hadar Member (KH). Like the SHT tuff, it occurs also in channels where glass shards are well preserved. Four submembers have been recognized within the Kada Hadar Member (KH-1, KH-2, KH-3, KH-upper), although the validity of these divisions has more recently been questioned (Johanson, et al., 1978). About 9 m above the KHT tuff is another distinctive marker, CC, consisting of a green argillite that produces small flakes as a characteristic alteration product of weathering.

The occurrence of complete and partial skeletons suggests rapid deposition, in a relatively low energy environment. The preservation is usually excellent, with some specimens looking almost like fresh bone, but many are

encased in a thin layer of hard calcified mud that may make cleaning and preparation difficult. Nearly all the specimens are surface finds, but their condition makes it clear that they have not been transported for any significant distance and the range of uncertainty regarding the horizons of derivation is usually small. However, it is not always possible to place material within one of the submembers, so localities which lie close to a boundary are designated by recording the two possible units (eg. DD2/3). The fossil localities are assigned numbers, prefixed by "AL" and each specimen from that locality is given an individual number (for example, the hominid skeleton "Lucy" is AL 288-1). The stratigraphic positions at present assigned to those localities that have furnished suid remains are indicated below. As will be seen, there are many localities in SH-1 to SH-3 and again in DD-1 to DD-3, but relatively few in SH-4 and in KH-1 to KH-3. It is convenient to group the suids stratigraphically into four divisions as follows:

- D. Lower Kada Hadar Member, together with two localities which span DD-3 and KH-1; includes localities: 120, 157, 164, 186, 310, 359, 361 and 367;
- C. Denen Dora Member, covering DD-1 (except those localities which also span SH-4), DD-2 and DD-3, including localities: 58, 116, 118, 121, 133, 134, 161, 162, 167, 168, 169, 171, 172, 174, 182, 184, 185, 187, 188, 190, 191, 194, 195, 201, 220, 233, 239, 241, 246, 247, 250, 259, 260, 287, 291, 296, 307, 309, 315, 316, 317, 321, 325, 332, 337, 342, 344, 358, 362, 378, 379 and 385;
- B. Upper Sidi Hakoma Member, embracing the localities within SH-3, together with those which span SH-4 and DD-1; includes localities: 53, 214, 226, 264, 266, 319, 330, 345, 347, 348, 380 and 384;
- A. Lower Sidi Hakoma Member, comprising localities assigned to SHT, SH-1, SH-2 and SH-3, together with those spanning both SH-3 and SH-4; includes localities: 107, 108, 109, 124, 125, 126, 127, 128, 129, 130, 131, 137, 138, 141, 142, 145, 147, 148, 165, 166, 175, 198, 199, 200, 204, 208, 217, 218, 222, 224, 225, 229, 232, 235, 248, 251, 252, 254, 255, 257, 263, 277, 327, 353, 360, 365 and 374.

There are at present no suids from the Upper Kada Hadar.

Much of the material is housed in the Ethiopian National Museum in Addis Ababa and the author is indebted to the Director, Ato Mamo, for allowing him

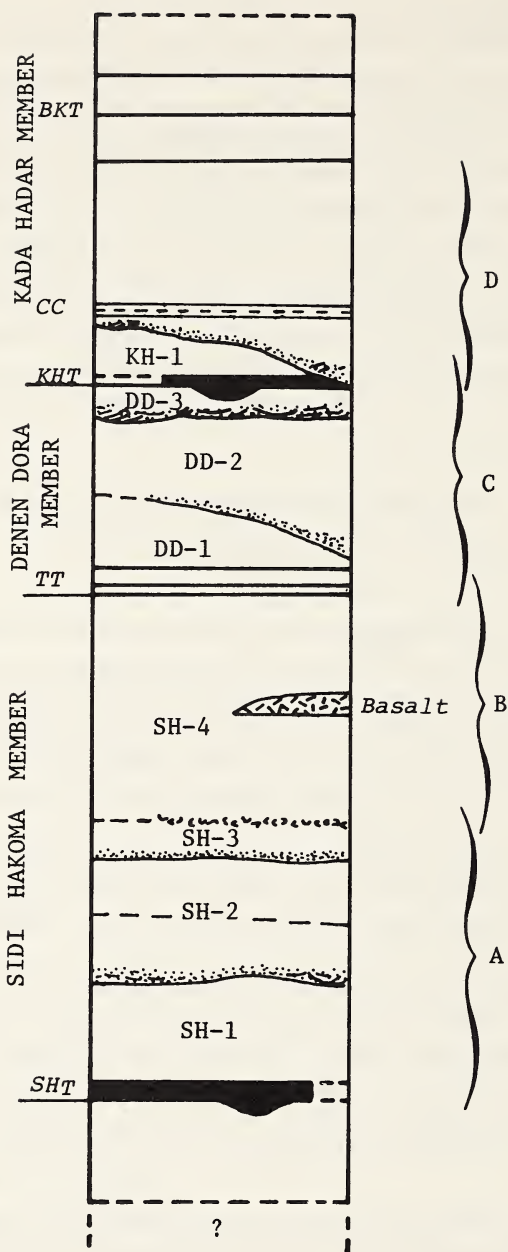


Fig. 1. Stratigraphic distribution of sites that have yielded suid fossil material from the Hadar area.

to work there, and to Ato Woldesenbet for considerable help in handling the material. Thanks are also due to Maurice Taieb, Yves Coppens and Don Johanson for inviting the author to study the suids from Hadar, and to Tom Gray for providing background data and invaluable help with the text. Support funds have been provided by the National Research Council of Canada, the Wenner-Gren Foundation for Anthropological Research, and the International Afar Research Expedition (IARE) and are gratefully acknowledged. A substantial debt is also due to Mr. Richard Wilding of the Archaeology Unit, University of Addis Ababa, for much help, advice and hospitality.

DESCRIPTION

Genus NYANZACHOERUS Leakey 1958

TYPE SPECIES: *Nyanzachoerus kanamensis* Leakey 1958

REVISED DIAGNOSIS: See Cooke and Ewer, 1972

Nyanzachoerus pattersoni Cooke and Ewer 1972

Material

BASAL MEMBER. Mandibular fragment with LM₂₋₃, AL 272-1.

LOWER SIDI HAKOMA. Almost complete skull with associated atlas vertebra, presumed male, AL 137-4 (SH-2); slightly damaged skull, presumed female, AL 107-13 (SH-3); incomplete skull, teeth broken, AL 235-2 (SH-2); palate and part maxilla with cheek teeth, except RP², AL 145-26 (SH-2); palate and part maxilla with partial dentition, AL 235-10 (SH-2); four maxilla fragments with two or more cheek teeth; four single upper teeth; good upper canine, AL 131-8 (SH-2). Damaged mandible with most of the teeth, AL 218-2 (SH-1/3); mandible with damaged symphysis, AL 126-8 (SH-2); symphysis and both mandibular rami with P₃-M₂ on both sides, LM₃ erupting, AL 365-9 (SH-3); left and right mandibular rami with complete cheek teeth AL 137-5 (SH-2); symphysis and left mandibular ramus with teeth, AL 127-15, AL 127-7 (SH-2); right mandibular ramus with RP₄-M₃, AL 165-14 (SH-2); four partial mandibles with several teeth, AL 142-13 (SH-2), AL 137-16 (SH-2), AL 126-65 (SH-2), AL 166-5 (SH-2); six mandibular fragments with two or more teeth, from SH-1 to SH-3, and one from SH-3/4; six mandibular fragments with single teeth; seven single lower teeth and two fragments.

UPPER SIDI HAKOMA. Partial skull with RP³-M³, AL 347-8 (SH-4); parts of broken skull with LM¹⁻³, AL 384-7 (SH-4); RM₃, incompletely erupted, AL 325-3 (SH-4).

DENEN DORA. Maxilla fragment with LM³, AL 134-14 (DD-2/3); isolated RM₁, AL 201-1A (DD-2).

Description

Nyanzachoerus is well represented in the collections up to the end of 1975, with approximately fifty cranial and mandibular specimens and a small amount of postcranial material, although the association is uncertain. The sample is larger than that from Kanapoi in northwestern Kenya, but matches very well in all respects. The two best skulls, AL 107-13 and AL 137-4, agree very closely with the female type and male paratype from Kanapoi, and both amplify and amend the interpretation of those specimens. They thus warrant individual description.

AL 137-4

This skull is very well preserved and has suffered only minor damage (Plate 1). The atlas vertebra is associated with the skull. The tip of the premaxilla and the tips of the nasals are missing. The top of the skull and most of the nasal area are intact, but both zygomatic arches have been damaged. The occiput is complete but there is damage to the auditory bulla and the ear region on the left side. The left upper canine is intact and the right upper canine is broken off at the alveolar margin. Both upper second premolars are broken off and the left dentition is damaged from the back of M¹ to the middle of M³. On the right side P³ is slightly damaged, as is M², but the dentition is reasonably complete. The dimensions and morphology of the skull agree almost perfectly with the paratype from Kanapoi wherever there are corresponding parts. The dimensions of the teeth match well with those of the male, and, as at Kanapoi, are somewhat more robust than the teeth of the female. They are less worn than the teeth of the paratype. Although the zygomatic arches in the Hadar specimen are broken, their roots are present sufficiently to show that the zygomatic arch flared out and was certainly as large as in the Kanapoi specimen. Comparative measurements are given in Table 1.

Of particular value in the Hadar specimen is the excellent preservation of the occipital and back of the cranial region of the skull, which were detached or missing in the Kanapoi paratype. In the Kanapoi specimen there was a part of the fronto-parietal area preserved and it is now clear that the restoration made by Cooke and Ewer (1972) is incorrect, as the skull is longer than had been expected. The parietal area is broad behind the orbits and is still broad at the constriction, about three-quarters of the way to the lambdoid crest. The occiput itself is long and the angle formed between the occiput and the parietal surface is only about 45°. In consequence, the occipital condyles do not lie very far behind

TABLE 1

Measurements of Skulls of *Nyanzachoerus pattersoni* (in mm)

	<i>Hadar Specimens</i>		<i>Kanapoi Specimens</i>	
	AL 137-4	AL 107-13	KP 239 Holotype	KP 264 Paratype
Vertex length	580+(633e)	+457(530e)	510e	620e
Basilar length	447+(490e)	+364(440e)	425	500e
Bizygomatic breadth	+270+	308	c270	c480
Frontal breadth	166	147e		
Parietal constriction	98	72.5	—	76
Crest breadth	155	108e		
Binaural breadth	202	180e		
Greatest breadth across nasals	62	—	53	71
Breadth of muzzle between infraorbital foramina	56e	—	48	66
Palatal length	320+(353e)	+230(305e)	301	352
Breadth of palate				
— between M ³ –M ³	43.0	35.0	33.0	40.0
— between P ² –P ²	71.5	40.2	52.5	73.0
Premaxilla breadth over I ³ –I ³	76e	—	69	95
Diastema I ³ –P ²		—	72	101
Diastema C–P ²	49	—	39.5	c35.0
Length of premolar series	56.5	50.3	51.9	68.0
Length of molar series	105.5	92.0e	95.2	99.1
Length of P ² –M ³	162.0	142.0e	147.0	161.6

e = estimated measurement; c = approximate measurement

the orbits when the skull is resting on the occlusal plane. The distance from the lambdoid crest to the condyles is not much less than the distance from the condyles to the back of M³. The specimen is a little crushed and it is possible that this sharp angle of the occiput is exaggerated by deformation, but even if that is true, the angle of slope is unusually sharp. The back of the occiput is fairly deeply scooped, much as in *Sus* and there is no sign of any median vertical rib. The upper part of the occiput is relatively flat and the wings do not sweep backwards as sharply as in *Sus*, but rather more like the condition in *Hylochoerus*. The ear region is notably wider than the rather narrow occiput, and the auditory canal emerges at an angle of approximately 45° from the horizontal. The bullae have been eroded away but the right paroccipital process is present and stout. The top of the braincase is depressed, and this was regarded

initially as an artifact. However, it has been noted in several skulls and may be a real feature of the genus.

The canine flanges are more or less intermediate in form between those of *Sus* and *Hylochoerus*. There is slight expansion of the nasals just behind the canine flanges, or, more correctly, above the back of the canine flanges, and there are slight signs of rugosity in this area reminiscent of the condition in the bush pig. The upper canine emerges practically parallel to the palatal plane, but sweeps outwards and upwards at the tip. It is truncated along much of the front face by a vertical wear facet. A broad ventral band of enamel occurs and is slightly striated parallel to the length, but not deeply grooved. There is also a posterior narrow inset enamel band but no indication of such a band on the upper anterior face. In cross-section, the canine is almost equidimensional with a squarish U-shape or broad heart shape with a shallow dorsal groove. Considering the massive size of the skull, the canines are relatively small. The cheek teeth conform to the pattern seen in the Kanapoi material except that the enamel is a little more complicated in P³ and P⁴. The upper left M¹ is worn to a flat surface of dentine, but the right one still has a perimeter ring of enamel. The enamel in the upper M² and upper M³ is thicker than it is in the female, corresponding again with features noted in the paratype material. The palatine notch lies only very slightly behind the back of M³ and is broadly rounded, although in some respects a little like a gothic arch. The basioccipital is fairly short, and the basisphenoid descends from it at a steep angle.

AL 107-13

This skull is well preserved, although the superficial bone is in a bad state. In size and morphology it is virtually a twin to the holotype from Kanapoi (Table 1). Most fortunately, it has preserved portions of the skull which were missing in the holotype (Plate 2 A/B). As in the holotype, the palate and cheek teeth are perfectly preserved, although the anterior premolars are missing in the Hadar specimen. The premaxilla, well preserved in the holotype, is missing from AL 107-13. The basicranial region, well preserved in the holotype, is badly damaged and only part of one occipital condyle remains in the Hadar specimen. The right side of the zygoma is missing, but the left zygoma is in excellent preservation. It differs from the type only in that the inflated marginal knob is better developed, and thus the front part of the zygoma projects more at right angles to the axis of the skull. The extra inflation is on the anterior external part of the knob, making it more like that of *Hylochoerus* and adding considerably to the broad platy area below and anterior to the orbit. In the holotype the whole of the upper surface, including the upper part of the occiput, the whole of

the top of the braincase and orbits, and the entire nasal region were missing. These are intact in the Hadar specimen and show that the nasal region was rather narrow, with the nasal bones up-arched; there is some lateral crushing and it is possible that the arching in the specimen may thus be exaggerated.

The parietal is moderately broad and the constriction between it and the lambdoid crest is wide. As in the male specimen, the braincase is hollowed and this increases the probability that this is the natural condition, somewhat resembling the braincase of *Hylochoerus*. Again as in the male, the upper part of the occiput is not deeply scooped, resembling that of *Sus* in general morphology, but the angle between the upper part of the occipital and the parietal surface is abnormally sharp. The rim of the orbits is raised a little above the level of the parietal, recalling the condition seen both in *Hylochoerus* and in *Phacochoerus*. From these raised orbits ridges extend down to at least the end of the lacrimals. The condition of the bone unfortunately makes it impossible to see the lacrimal sutures properly. Although the tip of the snout is missing, it would seem that the narrowest part of the maxillary area is in the vicinity of the infraorbital foramina, and the nasals widen anteriorly and tend to overhang the maxilla. The canine flanges are very similar to those in a male *Sus*. In the Hadar fossil the canine flanges are much more strongly developed than they were in the Kanapoi type.

The cheek teeth are slightly less worn than those of the holotype, but all the features are essentially similar. A minor difference is that in the holotype P³ the tip of the main cone is worn flat parallel to the grinding surface, whereas in the Hadar specimen the wear island runs obliquely from the tip back towards the P⁴. The P³ and P⁴ are also a little stouter and the anterior cingulum is not as strongly developed. The palate is a little wider at the positions of the second upper pre-molars. Essentially, therefore, the only difference between this specimen and the holotype is in the stronger inflation of the zygomatic arches. The bizygomatic width is consequently also a little greater. Both this skull and the male skull show that original estimates of the vertex length were too low, and the skulls are actually a little longer than was indicated in the publication by Cooke and Ewer (1972).

Upper dentition

No specimen occurs in which the upper incisors are preserved, so these teeth are still known only from the Kanapoi holotype.

The upper canine in the male skull AL 137-4 has already been described above. There are a few fragments of other upper canines and one almost complete left upper canine, AL 131-8, and the matching tip of the right canine,

AL 131-7. The canine in the skull measures 40.5 mm (vertical) by 38.8 mm (antero-posterior), whereas the isolated specimen is only 31.9 by 29.0 mm and has a length (in a straight line across the arc) of 130 mm. Although smaller than the male tusk, it is morphologically similar, with a broad ventral band of

Nyanzachoerus pattersoni

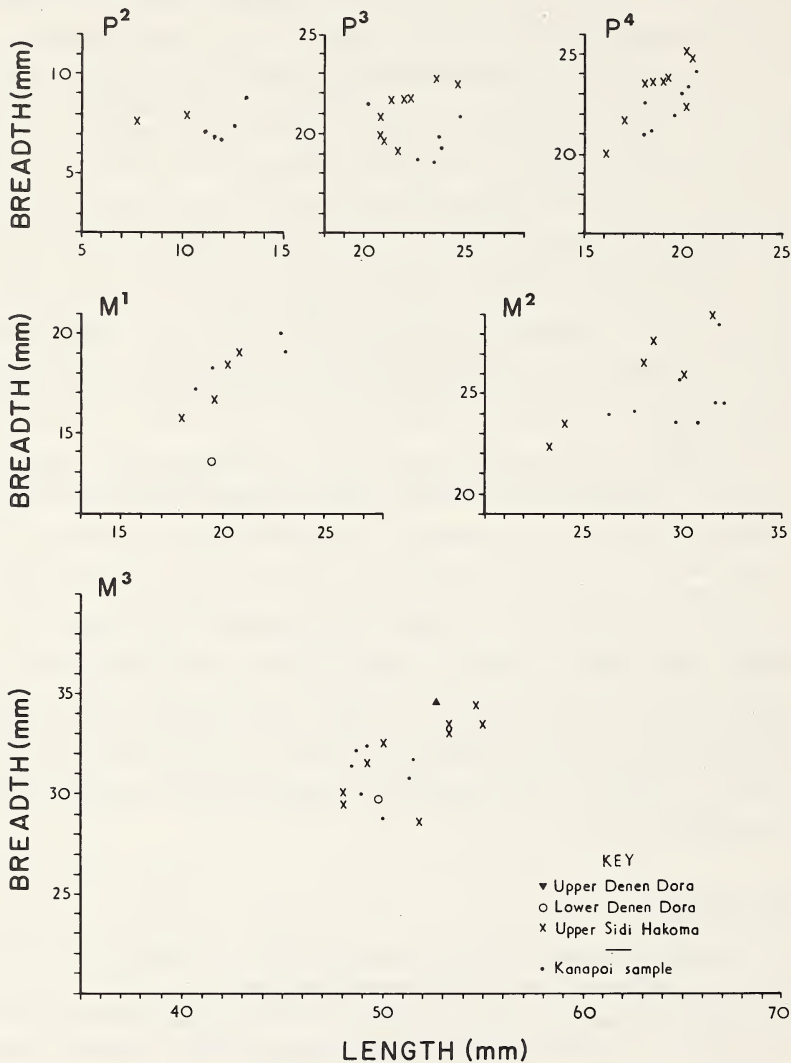


Fig. 2. *Nyanzachoerus pattersoni*. Length-breadth measurements on upper cheek teeth.

grooved enamel and a narrow inset posterior band. However, in this specimen there are traces of an anterior inset band as in typical *Sus*. The tooth is obliquely truncated by a long and slightly wavy wear facet.

Only two specimens of P^2 are known, and they are slightly smaller than in the Kanapoi material. P^3 and P^4 are well represented and their morphology and dimensions agree closely with the Kanapoi specimens. The same is true also for the molars, as will be seen from the plots in Fig. 2. A few of the upper third molars from Hadar are a little larger than those from Kanapoi, but the difference does not seem to be significant. The upper cheek teeth of AL 137-4 are shown in Plate 2 C.

Mandible and lower dentition

There are several good lower jaws that warrant particular description; all are from the Lower Sidi Hakoma unit. The most complete is AL 218-2, which corresponds in general with that of the paratype from Kanapoi, but is not quite as massive (Plate 3 A/B). It compares very well with the specimen KNM-KP 219, illustrated in Plate 4 of Cooke and Ewer (1972). However, it is more complete in that the entire symphysis is preserved with the two canines broken off a little way above their bases. The four central lower incisors are present, in very advanced wear, and the broken roots of the lateral incisors are also preserved. The anterior premolars are lost on both sides and there is some damage to the teeth, which are in advanced wear. There are no significant differences in the cheek teeth as compared with the Kanapoi material. The incisors are somewhat curious in that they are heavily covered in cement and show a ring of enamel surrounding a core of dentine. The same condition is observed in the incisor teeth of *Notochoerus* and suggests a link between these two genera. The symphysis is not wide but the incisors are arranged in a shallow arc. There is only a small gap between the lateral incisor and the canine but there is a long diastema between the back of the canine and P_2 . In cross-section the canines have a blunted V-shape, which is almost heart-shaped. They emerge from the symphysis at a very shallow angle. The symphysis itself is long, with the lower junction level with the back of P_2 . The ascending ramus is broken off and the back of the mandible seems very narrow for the massive jaw.

AL 126-8 is an excellent match for the holotype mandible in size, including the presence of the bases of rather small canines. The incisor area has been broken away and cannot be seen. The cheek teeth are well preserved on both sides and in fairly early wear (Plate 2 D). Both lower P_2 's are lost. The lower P_3 's have only the tips in wear and show a remarkably smooth anterior ridge with a distinct backward slope so that the tip of the crown lies over the rear

roots. The broken canine has a flat rear surface and is U-shaped rather than V-shaped, with enamel on all but the posterior surface.

AL 127-15 consists of a complete symphysis with the right P_2 and the whole of the left ramus with all the cheek teeth, while AL 127-7 is the matching right lower third molar in a fragment of mandible. The specimen is in excellent preservation and shows the symphysis extremely well. This is slightly larger than in the holotype mandible and the canines are already somewhat larger than in the previous specimen. The teeth are in early wear and it is possible that this dentition belongs to a young male, although it is not nearly as massive as the other specimen ascribed to a male. Five of the incisors are preserved. The two central incisors are smaller than the second incisors, as was the case with the holotype. The left I_3 is missing, but the right I_3 is present and is a very small tooth, relatively smaller than in the holotype. The central incisors have a strong median ridge on the upper surface and this is flanked by shallow grooves. The second incisors have a strong ridge on the outer side of the midline and the surface from the ridge to the medial side is a gentle slope, whereas on the outer side there is a decided groove. The canines are of moderate size and U-shaped in cross-section. They emerge at a strongly lateral angle, rising only gently above the horizontal plane. The cheek teeth are in early wear. P_2 is small and rather equidimensional. P_3 has the tip only just in wear and the peak lies above the center of the posterior roots. There are no other distinctive features which differ from previous material.

The lower cheek teeth are all well represented and the lengths and breadths of those complete enough to be measured are shown in Figure 3. The dimensions are closely comparable with the Kanapoi sample, although the third molars are, on the average, a little longer.

Discussion

The Hadar material increases very substantially the size of the sample of *Nyanzachoerus pattersoni* and adds to knowledge of some features of the species, especially in providing better evidence for the length of the skull and morphology of the dorsal surface. Although the third molars are slightly longer in the Hadar sample, this cannot be regarded as an indication of evolutionary or temporal trends. The combined Kanapoi-Hadar sample consistently displays a lower third premolar that is shorter and stouter than in the type of *N. kanamensis*, and M_1 is also notably longer in the latter species. In the Kanapoi sample the diastema between the lower canine and P_2 was only about 48-50 mm, compared with 67.5 mm in the type of *N. kanamensis*. In the Hadar sample, three of the lower jaws have diastemata in the range 62-64 mm, although others approxi-

Nyanzachoerus pattersoni

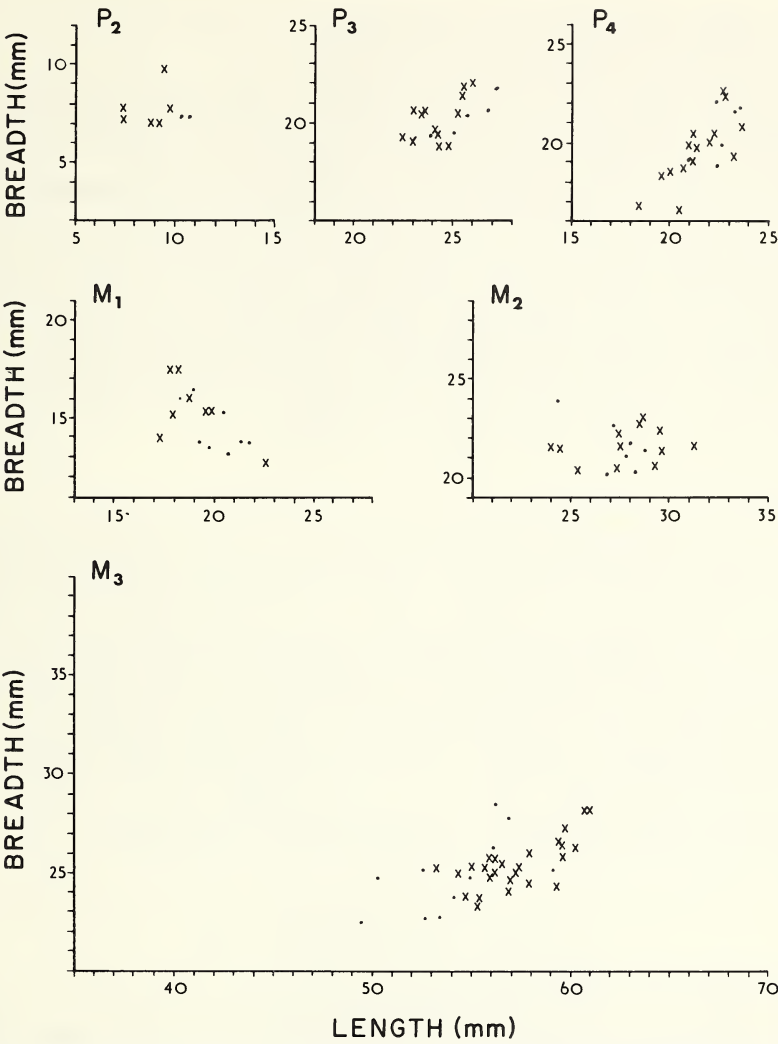


Fig. 3. *Nyanzachoerus pattersoni*. Length-breadth measurements on lower cheek teeth. Key as in Fig. 2.

mate the Kanapoi range. This diminishes the difference but until the elongate, narrow P₃ of the Kanam type can be matched, it seems preferable not to synonymize the two species.

Genus NOTOCHOERUS Broom 1925

SYNONYMY: *Gerontochoerus* Leakey 1943

TYPE SPECIES: *Notochoerus capensis* Broom 1925

NEW DIAGNOSIS: A genus of Suidae of large size, possessing hypsodont third molars in which the main lateral pillars are strongly folded, tending to produce dumbbell or H-shaped enamel islands, particularly in the lowers. Premolars reduced, with only the third and fourth premolars normally retained in the adult. P⁴ with small, closely appressed, paracone and metacone that are well separated from a small rounded protocone. Zygomatic arches robust and possessing thimble-shaped lateral projections in the male. Upper canines dorso-ventrally flattened, carrying a ventral enamel band, and flaring outwards in a strong flat curve not much above the palatal plane. Mandible robust with long, wide symphysis; anterior border almost straight and incisors small and well separated. Lower canines heart-shaped to U-shaped, at least in early stages of growth, and flaring laterally parallel to the uppers.

Remarks

The genotype species was founded by Broom (1925) on an isolated upper right third molar from the Vaal River gravels, South Africa. The tooth lacks an unknown amount from the anterior and was restored by Broom with an additional pair of laterals, making a total of five pairs (the last rather small) and six medians. The main lateral pillars have elongate, flattened outer walls and those on the lingual side are stouter and more complex than those on the buccal side, which are also displaced a little towards the front of the tooth. The tooth is moderately hypsodont, with the crown height more than one and a half times the maximum basal breadth. *Notochoerus euilus* differs from *N. capensis* in having fewer pairs of laterals and a lesser degree of hypsodonty.

Notochoerus euilus (Hopwood, 1926)

- 1926 *Hylochoerus euilus* Hopwood: 21; text-fig. 7; pl. 2, figs. 7-10.
1942 *Hylochoerus euilus* Hopwood; Dietrich: 108; pl. 17, figs. 114-126, 128, 130-136; pl. 18, fig. 149.
1958 *Notochoerus euilus* (Hopwood) (*partim*); Leakey: 31.
1958 NON *Notochoerus* (*Gerontochoerus*) *euilus* (Hopwood); Ewer: 357; text-fig. 11; pl. 4C, 5, 6.
1970 *Notochoerus euilus* (Hopwood); Cooke and Coryndon: 147; text-figs. 11, 12; pl. 7, A-E.

Emended diagnosis

A *Notochoerus* considerably bigger than the extant *Hylochoerus*. Upper third molars normally with three or four pairs of lateral pillars, lower third molars normally with four pairs of lateral pillars, plus a small terminal pillar or complex. Successive pairs of laterals separated by single strong median pillars; lateral pillars well separated from each other for most of their height, producing deep lateral valleys between them; cement well developed. Pillars strongly folded near the tips, producing stellate enamel islands in early wear; outer borders of lateral pillars rather flat and longer than the median lobe. Second molars much expanded antero-posteriorly above the base, somewhat as in *Phacochoerus*. Cheek teeth only moderately hypsodont, with maximum crown height in unworn upper third molars normally less than 1.3 times anterior basal breadth and in unworn lower third molars less than 1.5 times anterior basal breadth.

Material

Approximately 150 specimens represent substantial parts of skulls and mandibles, fragments, or isolated teeth that are measurable and there are also some 50 partial teeth. Listed below is a selection of the more important specimens in the collection.

LOWER SIDI HAKOMA. Damaged skull with RM^{1-3} , LM^3 , part LM^2 , AL 108-3 (SH-2/3); palate with P^3-M^3 both sides, AL 127-46 (SH-1/2); pair of mandibular rami with LP_4-M_3 , RM_{2-3} , broken RP_4 , RM_1 , AL 108-2 (SH-2/3); right mandibular ramus with RP_3-M_3 , AL 127-13 (SH-2); right mandibular ramus with RP_4-M_3 , AL 126-64 (SH-2).

UPPER SIDI HAKOMA. Two halves of palate with LP^3-M^3 , RP^3-M^2 , and left mandibular ramus with LP_3-M_3 , young adult, AL 53-44 (SH-3); damaged skull with LP^4-M^3 , RP^4-M^3 , snout lost, AL 171-1 (SH-3); left mandible with LP_3-M_3 (advanced wear), AL 58-13 (SH-4/DD-2).

DENEN DORA. (DD-2): Fine skull, occiput slightly damaged, with P^3-M^3 , both sides, AL 172-1; skull, damaged at occiput and lacking front of snout, and associated mandibles, lacking ascending rami, AL 342-9; damaged skull, lacking snout but with most cheek teeth, AL 167-15; maxilla with LP^3-M^3 and fragment with RM^3 , AL 158-28/29; left maxilla with LP^3-M^3 , and right maxilla with RP^3-M^3 (advanced wear), AL 330-1; damaged mandible with most cheek teeth, AL 174-2; mandible with symphysis, parts of canines and most cheek teeth, AL 174-4; damaged mandible with symphysis and incisors, AL 153-9; partial mandible with incisor sockets, LP_4-M_3 , RM_{2-3} , AL 168-2; (DD-2/3):

Left and right mandibular rami with LP_3-M_3 , RP_4-M_2 , AL 158-34; (DD-3): Partial skull, most teeth broken, AL 241-5; palate with P^3-M^3 , both sides AL 116-93; maxilla fragments with LP^{3-4} , LM^{2-3} , RM^3 , AL 116-54; fine mandible, almost complete AL 116-28 (may belong with AL 116-54); broken mandible with nearly all the teeth, AL 168-12; pair of mandibular rami with P_3-M_3 both sides, cracked, AL 185-4; right mandibular ramus with RP_3-M_3 , AL 174-1; broken mandible with LP_3-M_3 , RP_3-M_2 , partial RM_3 , AL 185-3; mandible, damaged anteriorly, with LM_1-M_3 , RP_4-M_3 , AL 378-1; damaged mandible with both canines, LP_{3-4} , LM_3 , RP_4-M_3 , AL 157-3; anterior palate with RP^{3-4} , AL 317-3A.

KADA HADAR. Damaged mandible with LM_{2-3} , RM_{2-3} , other teeth broken, AL 164-2 (KH-1).

Description

Notochoerus is not well represented in the Sidi Hakoma member but is abundant in the Denen Dora member, from which the best and most complete specimens have come. Although the form and structure of the molars have been known for some time, the present account constitutes the first description of the skull and mandible, and of the entire dentition.

The Skull

There are five good crania in the collection, as well as several less complete specimens or substantial parts of skulls. The most complete, which might be regarded as a sort of informal "type," is AL 172-1, from DD-2, which is virtually complete except for damage at the occiput and the loss of the canines and incisors (Plate 4). The vertex length is estimated as close to 580 mm when intact, as compared to about 430 mm in a good adult *Hylochoerus*. One other cranium, AL 108-3, from SH-2/3, appears to be roughly comparable in size, but the other three good specimens are more robust and have an estimated vertex length of approximately 610-620 mm. The more important measurements are given in Table 2.

The overall character of the skull is not particularly like any of the living suids, although in a general way it resembles the warthog, but without the exaggerated elevation of the braincase and orbits. There are also resemblances to *Nyanzachoerus pattersoni* and to the Kanapoi material referred to *N. jaegeri* (Coppens, 1971; = *plicatus*, Cooke and Ewer, 1972). The skull table is broad, with the frontal breadth ranging from a minimum of 166 mm in AL 108-3, to an estimated 230 mm in AL 167-15. The upper margins of the orbits are very

TABLE 2

Measurements of Skulls of *Notochoerus euilus* from Hadar (in mm)

	DD-2 AL 172-1	SH-3 171-1	DD-2 342-9	SH-2/3 108-3	DD-2 167-15
Vertex length	542+(580e)	+550(610e)	+440(c620e)	+395	+412+(c620e)
Basilar length	496	+483(510e)	+340(c520)	+320	+340
Bizygomatic breadth	392	—	c380e	166	c230c
Frontal breadth	187	175e	c200e	49	74
Parietal constriction	50e	—	59	135e	178
Crest breadth	—	—	—	192	234
Binaural breadth	183	185	c62e	—	—
Greatest breadth across nasals	57	77	—	—	—
Breadth of muzzle between infraorbital foramina	c65e	70e	c80e	—	—
Canine flange breadth	163.5	—	c320e	+152	+205
Palatal length	369	—	—	—	—
Breadth of palate	46.7	51.5	59.0	46.7	53.7
—between M ³ -M ³	53.1	58.0	79.0e	—	67.3
—between P ³ -P ³	50.5	—	—	—	—
Premaxilla breadth over I ³ -I ³	175	—	—	—	—
Diastema I ¹ -P ³	74	—	—	—	—
Diastema C-P ³	29.8	31.5	—	—	—
Length of premolar series	111.6	119.1	—	129e	33.0
Length of molar series	141.4	150.0	—	—	131.7
Length of P ³ -M ³	—	—	—	—	164.0

slightly elevated above the top of the braincase, which is gently concave between the eyes and flat behind them. Behind the eyes, the temporal crest sweeps rather sharply inwards, not quite as abruptly as in the antero-posteriorly compressed braincase of the warthog, but a little more abruptly than in the bushpig. As in both these suids, the breadth at the occipital crest is wide, unlike the condition in *Sus*. The parietal constriction is narrow and lies far back on the braincase, quite unlike the condition in *Hylochoerus*. The occiput itself is deeply scooped and resembles that of *Potamochoerus porcus*. There is no median ridge (Plate 3 D).

The slight ridges that form above the orbits are continued in front of the eyes as ridges that flank the supraorbital foramina, very much as in *Nyanzachoerus* and also in the forest hog. The nasals are straight and parallel-sided almost to the level of the canines before tapering to their tips. The muzzle is shaped very like that of *Nyanzachoerus*, with the nasals convexly curved and joining the upper edge of the maxillae to form a fairly sharp edge that may overhang the sides of the snout. The maxillae then curve outwards gently to the border of the palate. Anteriorly, the lower part of the maxillae expands progressively to form the sheath that surrounds the canines, in general rather like that of the forest hog. The resemblance to the forest hog lies in the basic shape of the flange, particularly in the form of the dorsal surface, which is broad with a low lateral crest. However, the canine emerges in a less lateral direction, as the alveolar margin is oblique to the axis of the skull instead of almost parallel to it. Anteriorly the palatal part of the flange extends forwards and is continued as an unusual feature in the form of a lateral shelf that borders the front of the snout, including part of the premaxilla. Posteriorly, the flanges curve smoothly into the root of the zygoma, much as in the warthog, with the infraorbital foramina at the junction; however, the flanges do not have the tubular character of those in *Phacochoerus*. On the palatal aspect, the expanded area has much the shape seen in the forest hog but is tapered forwards by the anterior shelf described above; this makes the premaxilla look shorter than is actually the case.

The root of the zygoma begins just behind the infraorbital foramen and curves smoothly outwards very much as in the warthog until it is at an angle of about 45° to the axis of the skull. It then changes direction and commences a second, rather gentle, curve recalling the form seen in a more exaggerated manner in the warthog. This is complicated by the presence of large thimble-shaped lateral protrusions (or knobs) that project from the jugal area and these tend to obscure the fact that the temporal portion of the zygoma is in a normal position; without the "knobs" the zygomatic arch would be much as in a female *Hylochoerus*. These curious and characteristic lateral protrusions are approximately at right angles to the axis of the skull when viewed from the dorsal

aspect, but from the front or back they can be seen to droop down until their rounded tips are close to the palatal plane (see Plates 3 C, 4). The protrusions seem to consist of hollow bone, and when they are broken away, as is usually the case, it is very difficult to be sure whether they existed or not. Consequently, it is not certain whether they occur only in the males, as might be expected; in one of the skulls AL 171-1, the lower border of the right zygomatic arch seems to be intact and it appears as if no knob existed. In all the other skulls, the survival of the outwardly flared bases of the knobs betrays their existence.

As a result of some elevation of the back of the skull, although not nearly to the extent seen in the warthog, the area below the orbits is broad and platelike. In most of the specimens the area where there would normally be the hollow for the origins of the levator rostri muscles is crushed in and seemed to consist of very thin bone with a sinus space below it. However, two of the skulls show that, far from being scooped out for the muscle insertions, this area was inflated in a manner resembling that of the so-called "lacrimal bulla" in the ox. The same feature is shown by specimens from the Omo area and appears to be a diagnostic characteristic. The attachment areas for the depressor rostri muscles are weakly scooped and it must be inferred that *Notochoerus* did not use its snout for rooting.

One of the skulls, AL 108-3, although lacking the whole of the snout and premolars, is important as it belongs to a young adult; the sutures in the lacrimal area are still open and it is possible to examine the shapes of the major bones. The lacrimal is quite narrow and the lacrimal/parietal suture is high up on the eye socket. The orbit has a strong indentation at the antero-lower edge, often also seen in *Sus*, and the lacrimal extends down into this notch. The lacrimal then widens and runs along the upper crest line in an arch and does not apparently come into contact with the nasals until well in front of the nasal-frontal suture. As the skull is broken at the critical point, it is not clear whether the lacrimal ever does come into contact with the nasals or whether it stops short, although the latter interpretation seems the more likely. The lacrimal is thus a rather elongate, somewhat oval-shaped bone, and it does not show any area of depression for the attachment of the narial muscles. The suture between the maxillary and the jugal is very far forward and lies across the bulging area that has already been noted above. The bulge has collapsed because of the thin nature of the bone.

This same skull has the occiput well preserved. The frontal area is flat, as in other specimens, and the parietal is short and narrowed, much as in *Sus*. The parietal constriction is narrow and *Sus*-like, with the braincase expanding below it. The occiput itself is not very high and is relatively wider than in *Sus*,

but not as deeply scooped. The wings do not project diagonally backwards as they do in the modern pig, but spread laterally as in the bushpig and forest hog; there is no median ridge. When the skull is set in the occlusal plane, the occiput is only about 20-25° off the vertical, and the surface of the temporal condyles lies about level with the top of the foramen magnum. The temporal condyles trend almost perpendicular to the axis of the skull and in consequence, the back of the zygoma, where it bends up to the auditory region, is farther behind the orbit than in *Sus*. The occipital condyles are not elevated abnormally above the palatal plane and the general appearance of braincase height in the skull is achieved by a relative increase in the elevation of the orbits, as well as by the height of the zygomatic area of the maxilla. The ear region is also high and wide, though not to the extent seen in the warthog, and the auditory canal points diagonally upwards at a rather steep angle, perhaps as much as 50° from the horizontal.

The basicranium is poorly preserved in most of the specimens. As far as can be seen, the auditory bullae are relatively small and are strongly compressed laterally. They are very narrow and pointed anteriorly and are directed obliquely towards the center of the palatal notch. The mastoid and paramastoid processes are strong and the paramastoids very stout (and probably also long).

The palate has a general resemblance in shape to that of the forest hog, no doubt dictated by the need to accommodate the extremely large canines. The premaxilla is relatively narrower than in the forest hog and resembles to some extent the corresponding region in the warthog. However, the border of the palate curves smoothly into the expanded area in front of the canines and does not show the abrupt change of angle or notch seen in most other suids (Plate 4). Only one pair of incisors was present and there is no trace of sockets for other incisors. The teeth themselves are not known but the sockets indicate that they were relatively smaller than in the forest hog and comparable with those in the warthog. The anterior palatal foramina are of moderate length and are laterally compressed. The canines emerge very much as in forest hog or warthog, but lie very nearly in the palatal plane. Behind this expanded area, the palate narrows gradually to the point where the canine sockets end and the palate is narrowest just in front of the anterior premolar (normally P³). The posterior palatal foramina lie about opposite the midpoint of the third molars and from them the usual blood vessel grooves run forwards, diverging at the level of the canines and then converging again to their termination at the anterior palatal foramina. The palatine notch lies well behind the back of the third molars.

The canines are large and fairly strongly curved, comprising an arc that may be as much as one third of a circle, as is also the case in the male forest hog or warthog. However, their orientation is different as they extend horizontally

almost in the plane of the palate, with only a small rise at the tips. In cross-section they are unusual as the normal suine structure has been distorted by oblique flattening, with the dorso-ventral dimension only about two thirds to three quarters of the antero-posterior one. On the dorsal surface there is a broad shallow groove and on the antero-ventral surface there is a strongly marked groove that lies almost directly below the dorsal one, making the cross-section rather like a figure 8 on its side, with the smaller loop anteriorly. The posterior face is weakly grooved, thus turning the "lazy 8" into a form that can best be likened to an inverted squashed bell shape (see Figure 4). The ventral band is

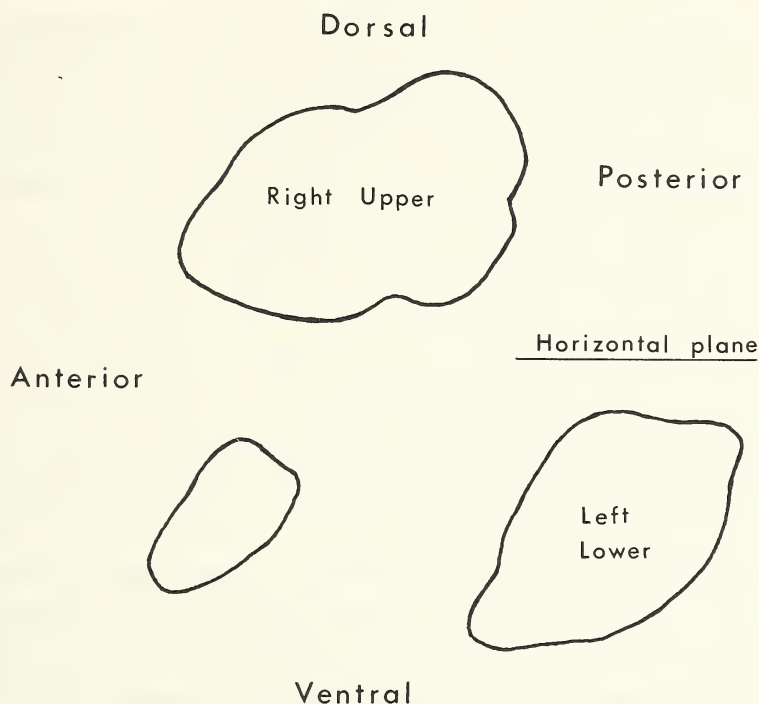


Fig. 4. Outline cross-sections of upper right canine (top) and lower left canines (below) of *Notocherus euilus*. The top and lower right drawings are taken near the alveolar margin; the lower left drawing is near the tip. Natural size.

made of ribbed enamel and there are narrow inset bands of enamel on the antero-dorsal and postero-dorsal "edges" of the tooth. However, in some specimens the whole tooth is longitudinally ribbed, although only the ventral part has enamel.

In all but one of the skulls and palates, there is no sign of an upper P^2 and no scars that might represent P^1 are found in the fairly long diastema between the canine and P^3 . The same is true of the mandibles and it is clear that only $P^3/3$ and $P^4/4$ are normally retained in the adult. However, AL 342-9 (from DD-1/2) consists of a good skull and associated mandible, a little distorted by oblique pressure, and it is a young adult with the third molars in wear anteriorly but not fully erupted posteriorly. The P_2 is retained on both sides in the lower jaw but the palate is broken across just in front of the upper P^3 's and the presence or absence of P^2 cannot be stated with certainty. If P^2 was present, as seems likely, it must have been separated from P^3 by a gap of at least a few millimetres.

In this skull, AL 342-9, the bone is badly cracked and postmortem distortion has separated the teeth so that the contact facets between them are now from 2 to 8 mm apart (RM^3 has been crushed back into its socket and is 19 mm from the back of RM^2). The P^3 and P^4 in this specimen are in early wear and are fairly typical. P^3 is a subtriangular tooth comprising two external elements (paracone and metacone), lying obliquely to the axis of the tooth row so that the paracone is on the midline. The postero-internal corner is buttressed by a strong oval protocone, separated from the paracone/metacone by a wide and deep fovea, open on the antero-internal side. The back of the fovea is closed by one or two high cingulum cusps. Anteriorly there is a moderately low cingulum band. P^4 is rounded in outline and the crown is about as high as the transverse diameter. The external face shows only the faintest sign of a groove that divides the crown at the tip into paracone and metacone islands. The protocone is rounded and relatively small and is separated from the paracone/metacone by a narrow but well developed transverse valley, closed off posteriorly by a high but thin cingulum. There is a modest anterior cingulum. From the transverse valley, a distinct indentation marks the division between paracone and metacone and there is a matching shallow groove in the protocone, giving a slight + -like form to the valley. In other specimens, the paracone/metacone in P^3 may appear virtually as a single cone. In P^4 the area in the center of the valley may form an isolated pit as advancing wear of the anterior and posterior cingula closes off the valley. There is also a tendency for the three cones to become more columnar in some specimens.

In most of the skulls, even in the young adult AL 342-9, the upper first molar is very worn and the pattern is difficult to discern. It soon becomes a stump of dentine and M^2 moves forward as M^3 erupts behind it, much as is the case with the warthog. In teeth in early wear, M^1 is seen to be formed of two well-developed pairs of laterals, with a single median between them, a weak anterior cingulum complex, and a modest posterior cingulum complex. The

tooth is longest in early wear and becomes almost equidimensional as wear proceeds.

The upper second molar is moderately high crowned and has its maximum length in early wear, when only the tips of the enamel pillars have been abraded. From the base, the anterior face rises forward and the back bulges upward, much as is the case with the more hypsodont second molars of the warthog (Fig. 5). The third molar is initially "tucked in" under the greatly expanded

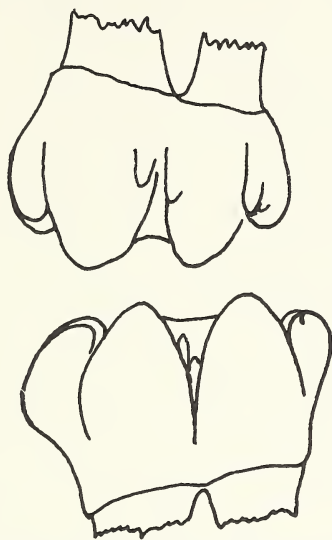


Fig. 5. Sketches to show the lateral aspects of upper (top) and lower (bottom) second molars of *Notocherus euilus*, indicating the substantial posterior bulge of the large cingulum complex. Natural size.

posterior cingulum complex. The crown length thus decreases with advancing wear and the posterior complex shortens, but the second molar remains an elongate tooth even in advanced wear. As far as possible, measurements are taken at the base of the crown so as to facilitate comparison by minimizing changes in the occlusal length with age. The basic structure of the tooth is like that of M^1 but the cingula are better developed, especially the posterior one. The form of the lateral pillars is essentially like the anterior part of the M^3 .

The upper third molars consist essentially of three well-developed pairs of large lateral pillars, followed by a terminal complex that ranges from three small pillars to a good fourth pair, the former being more normal. Very often there is a well-developed fourth lateral pillar on the external (buccal) side but only a small one on the lingual side and the lingual pillars are not level with their

mates but are displaced a little posteriorly. The space between the first and second laterals is wider on the buccal side than on the lingual one. A single median pillar lies between the first and second pairs of laterals, but there may be one or two medians between the second and third pairs. The first and second pairs of laterals are in contact at the midline but the third and fourth pairs may be separated by the partial intervention of the medians. There is an anterior cingulum complex, broken up into several small columns, the center one being almost the size of the medians and forming a wedge between the front pair of laterals. There is usually a stout central terminal pillar at the back of the tooth, but this may sometimes be displaced towards the buccal side and be accompanied by an additional small terminal pillar. In early wear, the lateral pillars show stellate enamel islands, but as wear proceeds, two of the grooves become dominant and divide the pillar into a lateral lobe and a median lobe. The lateral lobe has a relatively smoother outer rim of thicker enamel than is the case in the remainder of the island, although there is sometimes a thin external groove or indentation in the wall of the lateral pillar. The median lobe is less regular and retains some of the stellate appearance by having three or even four "points" initially; but with wear the grooves diminish and the enamel island as a whole becomes progressively more like a dumbbell or H-shape, although minor irregularities may persist on the median lobes, especially in the lingual pillars. The H-shape is best developed at the front of the crown and tends to become distorted in the columns nearer the back, with the median arm of the H displaced forwards. In general, the median area of the H tends to be a little shorter than the lateral one. Minor folds diminish with advancing wear and the pattern becomes very simple. The central, or median, pillars also form stellate enamel islands initially but these become oval or irregularly oval as wear proceeds. Measurements are plotted in Fig. 6 and examples are illustrated in Plates 5 and 6.

Another feature of variation within the Hadar sample is in the degree of upward taper of the crown from the base to the occlusal surface. In general, the occlusal breadth is a good deal less than the maximum breadth of the tooth at the base of the enamel. As the crown height of unworn third molars is not much greater than the anterior basal breadth, the lower crowned variants tend to have a more or less trapezoidal transverse cross-section at the front of the tooth, the broader the base the greater the tendency. In the narrower molars, the sides of the crown are more nearly vertical, although there is always some degree of upward narrowing of the crown. Some individual teeth may resemble the molars of *Nyanzachoerus jaegeri* but are usually distinguishable by the greater development of the talon (*N. jaegeri* has only three pairs of lateral pillars, the third often weak) and by the shape of the enamel islands, which in *N. jaegeri* are more M- or W-shaped than H-shaped. If premolars are present in the

Notochoerus euilus

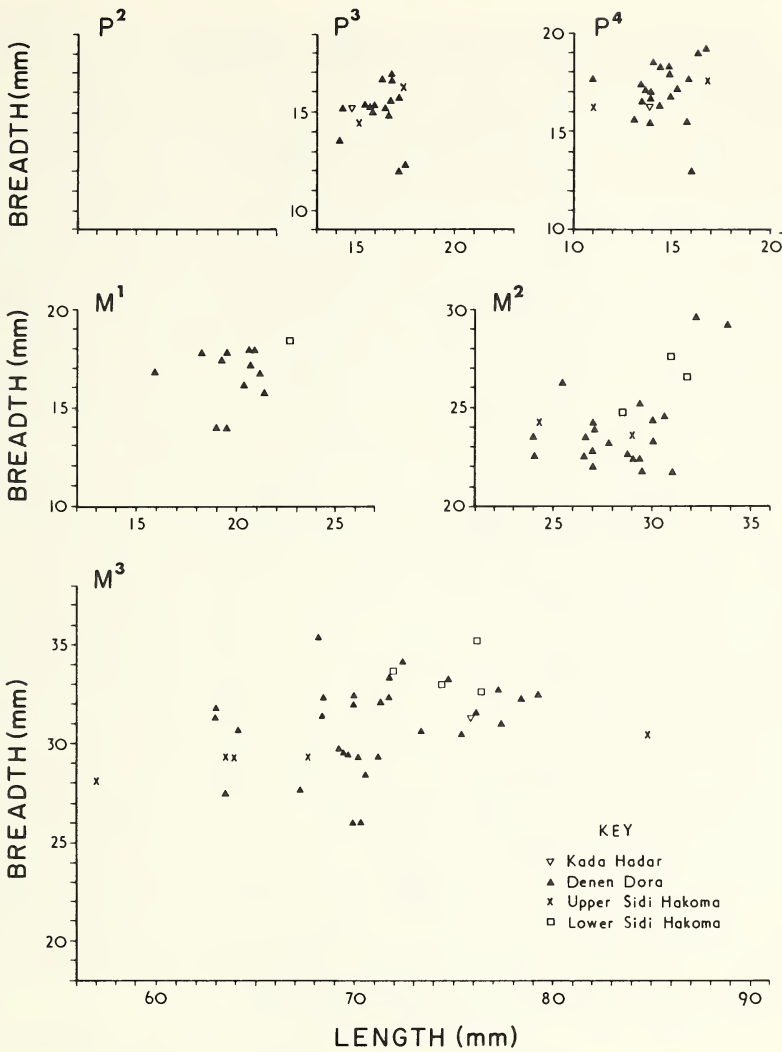


Fig. 6. *Notochoerus euilus*. Length-breadth measurements on upper cheek teeth.

specimen, the P³ is substantially smaller and P⁴ somewhat smaller in *Notochoerus euilus*. However, the morphological resemblances suggest a close genetic relationship between *N. euilus* and *Nyanzachoerus jaegeri*, and there may be some risk of misidentification in certain isolated specimens.

The Mandible

The lower jaw is represented by several specimens that are reasonably complete except for the invariable loss of the ascending rami. AL 116-28 (from DD-2/3) is probably the best specimen, with the incisors and canines preserved on both sides and a full complement of cheek teeth (Plate 7). The symphysis is long, although there are other specimens that are longer, and it is very wide and spatulate across the canines, very much as in the forest hog. The anterior border is almost straight—even more so than in forest hog—and all six incisors are present (Plate 8 A). They are very much reduced, almost peglike in character, and are strengthened by abundant cementum. The lateral incisor is an absurdly small tooth for a jaw of this size and it looks almost like a first premolar, embedded in a thick shaft of cement. The central incisors are very worn and were probably smaller and shorter initially than those in a modern domestic pig, (the skull of which is only half as large as that of *Notochoerus*); only the bases remain as stumps, about the size and shape of a human incisor and thickly covered with cement. The second incisors are morphologically like shortened *Sus* teeth, of which only the bases remain. Only a few other lower incisors are known, including an RI₁ belonging to the associated skull and mandible AL 342-9 (DD-2) which is a young adult so that the incisor is very little worn. The length of enamel on the anterior (lower) surface is only 14.5 mm and on the upper surface is 22.3 mm along the broad median ridge, while the transverse diameter at the base of the enamel is 8.0 mm and the antero-posterior dimension at this position is 9.3 mm. This is a little more robust than in *Sus scrofa* or *Potamochoerus porcus*, but very much shorter. The median posterior rib is broader and less marked than in *Sus* and the morphology is more like the I₂ than I₁ in the living form. It is more nearly comparable with the corresponding tooth in the forest hog. In this specimen the heavy cement coating is not present, but may have been lost. The whole symphysis in this specimen is very like that of AL 116-28, as also is AL 153-9 (DD-2) in which the broken roots of the four central incisors confirm the small size of these teeth and the two tiny lateral incisors are preserved, with their premolarlike morphology. Ventrally, the symphysis is also rather like that of the forest hog.

In AL 116-28 the canines are intact and emerge from the symphysis at a very low angle, not much above the occlusal plane. They are robust and essentially flattened oval in shape, measuring 42 mm by 27 mm at the alveolar margin, with the long axis antero-posteriorly oriented. The surface is covered with thin enamel, except on a slightly flattened posterior surface. The teeth are fairly sharply curved and carry only a very small anterior wear facet that may be due to use rather than to attrition against the uppers (Plate 8). Other specimens confirm both the form and the attitude of the canines, although in AL 174-4

(DD-2) there is no enamel on the upper face or on the flattened area at the back of the tooth.

In AL 116-28, and in most of the other specimens that include canines, there is a long diastema between the back of the canine and the anterior premolar, which is normally P_3 . This tooth lies just about level with the junction of the two halves of the symphysis. In this specimen there is no trace of P_2 or of a healed scar, despite the excellent state of the bone. The same is true of other specimens, although in most of them the bone is damaged and a scar might easily be missed. However, in the mandible of the young adult, AL 342-9, P_2 is present on both sides. It is a very small tooth, about half the length of the P_3 , and is relatively wide. It consists of a single stout cone with a smooth anterior face, but having a thin ridge running to the back of the crown. The disparity in size between the P_2 and the P_3 is reminiscent of the relationship found in *Nyanzachoerus*. The P_2 is a little stouter than P_2 in *Sus scrofa*, but is of comparable absolute size, whereas P_3 is 50% larger.

The P_3 is represented by a good number of specimens, for which length-breadth plots are given in Figure 7. Also shown are plots for P_3 in *Nyanzachoerus jaegeri* and it will be seen that this tooth is considerably smaller in *Notochoerus euilus*. However, two specimens from the Sidi Hakoma unit are of comparable size. AL 124-5, from the lower Sidi Hakoma, consists only of P_3 and P_4 and its identity is not certain. The other, AL 174-1, comes from the upper Sidi Hakoma, but the third molars are larger than those of *Nyanzachoerus jaegeri* and their morphology is typical for *Notochoerus*, and its length (82 mm) suggests that it is a large *N. euilus*, although this is not certain. Morphologically, the P_3 is moderately elongate and comprises a stout single cone with a smooth anterior face that slopes backwards so that the tip lies over the front of the rear root. There is a well-formed posterior cingulum, half the height of the crown, marked off from the main cone by a weak groove lingually and a stronger one buccally. The P_4 is wider than the P_3 but often slightly shorter, so that it appears almost equidimensional. It also consists of a stout main cone, with the tip practically central, but there is a well-formed, fairly narrow, anterior cingulum and a strong posterior cingulum, or complex, that extends at least three quarters of the height of the crown, much as in *Nyanzachoerus*. In some specimens, especially those in early wear, the tip of the main cone is divided into two elements, the anterior one slightly on the buccal side of the midline, and the posterior one slightly on the lingual side. Because of this slight asymmetry, the posterior cingulum is marked off from the main cone by deep lateral grooves, of which that on the buccal side is the deeper, whereas weaker grooves flank this anterior cingulum and the deeper lies on the lingual side. There is a distinct anterior ridge in most specimens, but it disappears with wear and an anterior cingulum pillar may appear.

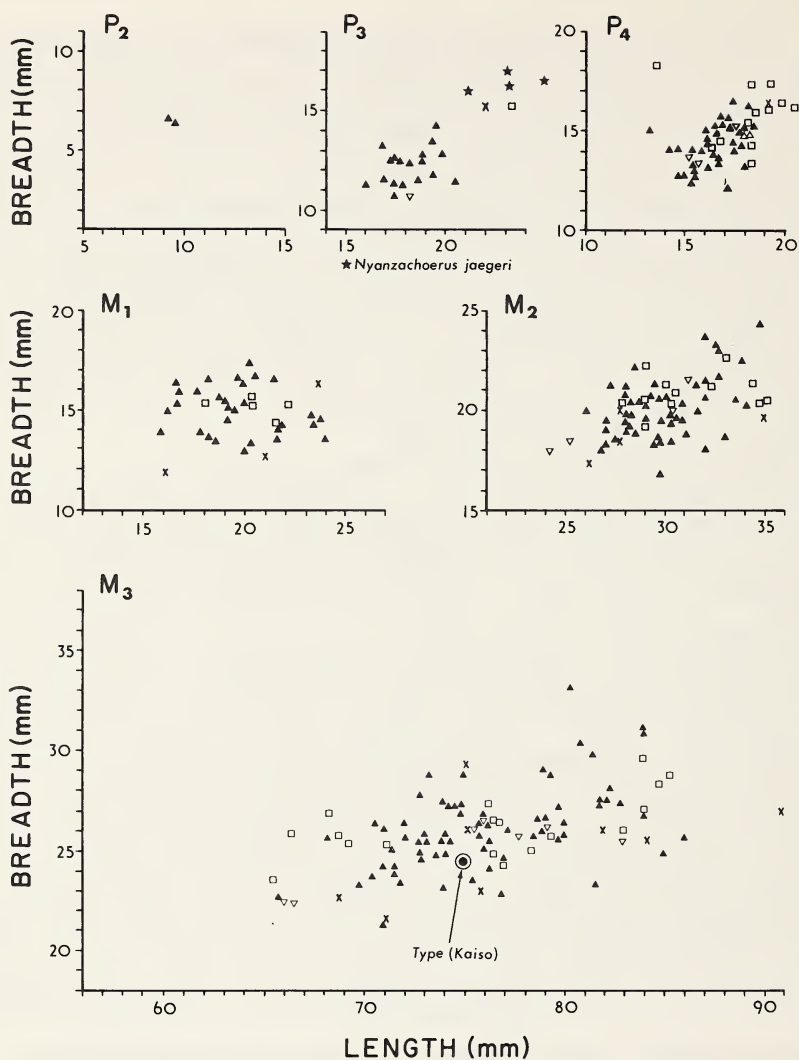
Notochoerus euilus

Fig. 7. *Notochoerus euilus*. Length-breadth measurements on lower cheek teeth. Key as in Figure 6. Data for the P₃ of *Nyanzachoerus jaegeri* and for the Kaiso type of *Notochoerus euilus* are also shown.

The first molar is usually worn to dentine with remnants of enamel but its structure is essentially like that of M₂, except that the posterior cingulum is

weaker. In early wear it is a narrow, elongate tooth, but it broadens and shortens with advancing wear. Dimensions are given in Figure 7.

The M_2 is an elongate tooth with a well-developed posterior cingulum complex comprising a median pillar and two posterior columns that look almost like an incipient third pair of laterals. There is also commonly an accessory basal pillar on the buccal side behind the second external lateral pillar. There is a weak anterior cingulum complex but it is obliterated when the tooth is only half worn. The first paired laterals are usually not quite mirror images, the lingual one being the larger and wearing to an enamel island that may be more X-shaped than H-shaped, while the buccal one sometimes becomes mushroom shaped through lack of the median arm of the H. The second pair of laterals is usually more symmetrical and the islands approximate an H-shape, although the median arm is normally shorter than the lateral one and there is a distinct indentation, or groove, on the median side. The lateral pillars may be angled slightly forwards relative to the base of the crown, when viewed from the side. The anterior and posterior complexes bulge outwards, somewhat in the manner seen in the more hypsodont teeth of the warthog, so the maximum crown length is reached when only about one-fifth of the original height has been worn away (Fig. 5). The anterior complex of M_3 fits under the posterior bulge of M_2 and comes into wear after M_2 has passed its maximum length. The M_3 rotates into position by completion and elevation of the posterior columns and as it grows and abrades, the space between it and the back of P_4 diminishes progressively until the whole of M_3 is in full wear. From a functional viewpoint, the effect is to maintain a reasonably consistent length of molar grinding surface from the young adult, with only the front half of M_3 in wear, to the older adult, with M_1 - M_2 shortened, but the whole of M_3 in use.

The lower third molar normally consists of four well-developed pairs of lateral columns and a terminal complex consisting of three columns, two of which form an incipient fifth pair of laterals; in some specimens these two columns are sufficiently developed to constitute a fifth pair of laterals. Each pair of laterals is well separated from the next pair by wide lateral grooves and by a stout median pillar. As in the uppers, the laterals form moderately stellate enamel islands in early wear, although dominant anterior and posterior clefts soon divide the pillars into external and median lobes. On the first two pairs, an H-shaped enamel island develops with further wear, initially with the two lobes of the island sub equal in size but, as wear proceeds, the lateral lobe may become relatively longer than the median one. On the succeeding pairs, the stellate form persists longer and the H-shape is less obvious. In some teeth, the posterior cleft may dominate so that the shape becomes almost an inverted U. The disparity between basal breadth and occlusal breadth is not as great as in the

uppers, so that the sides of the crown do not taper markedly. The greatest breadth at the base of the crown is often at the second pair of laterals rather than the first. The median pillars form more or less equidimensional enamel islands, initially stellate but becoming oval with wear. The anterior complex is weakly developed. The hypsodonty is moderate with the maximum crown height less than 1.5 times the maximum basal breadth. Length/breadth ratios are plotted in Figure 7 and examples of the lower dentition are shown in Plates 7 and 8.

Discussion

The Hadar collection provides a substantial sample of material that can be ascribed with some confidence to *Notochoerus euilus* as the features of the original syntypes from Kaiso fall well within the range of variation encountered in the Hadar material. If the reconstruction of the holotype RM₃ by Cooke and Coryndon (1970) is approximately correct, it would lie about in the middle of the range observed for M₃ (see Fig. 7). However, those authors considered that material from Laetolil, in Tanzania, differed from the Kaiso species and they referred it tentatively to *Notochoerus* cf. *capensis*. The writer has re-examined this material in East Berlin and, in the light of this study and the variations encountered in the Hadar sample, it is concluded that Dietrich's (1942) original identification as "*Hylochoerus*" *euilus* should stand.

The Hadar sample, although large, comes mainly from the Denen Dora member of the succession and the samples from the other members are rather inadequate for statistical comparisons to be useful. In general, the range for the molars from the Denen Dora would include all the samples from the earlier and later horizons, the only exception being an unusually small M₃ from the upper Sidi Hakoma member. However, for the upper premolars this is less true and there is a suspicion that the specimens from the Sidi Hakoma member may be larger than those from the Denen Dora. From a morphological aspect, the premolars from the Sidi Hakoma are more robust and *Nyanzachoerus*-like than those from the higher members, and there seems to be a change towards higher crowned and more delicate premolars in the upper part of the sequence. The frequency of occurrence of third molars with a strong upward tapering of the crowns also diminishes in the successively higher horizons and the molar structure seems to become more stable and "typical."

From the Usno Formation in the Omo area of southwestern Ethiopia, there is a large sample of material assigned to *Notochoerus euilus* by the present writer but the description is still unpublished, apart from some measurements on the third molars (Cooke, 1976). The range of size variation in the third molars in the Usno sample is almost identical with that for the Hadar material.

However, in the Hadar specimens the enamel is generally thick and does not show the thinning in the folded portions of the lobes that is seen in the Usno material. As a result, the Hadar teeth seem to be less complex in their folding, even in the early stages of wear.

The structural features of the dentition suggest that *Notochoerus* is related to *Nyanzachoerus* and is closest to *N. jaegeri*. The premolars are further reduced in size compared with the latter, but the disparity between P_2 and P_3 remains as evidence for the trend and relationship. The third molars are further enlarged, as compared with *N. jaegeri*, thus increasing the grinding area, but they remain relatively low crowned.

Genus KOLPOCHOERUS E. C. N. and H. E. van Hoepen 1932

SYNONYMY: *Mesochoerus* Shaw and Cooke 1941; *Omochoerus* Arambourg 1942; *Promesocherus* Leakey 1965; *Ectopotamochoerus* Leakey 1965.

TYPE SPECIES: *Kolpochoerus paiceae* (Broom 1931) (syn. *K. sinuosus* E. C. N. and H. E. van Hoepen 1932).

Diagnosis: Suidae of moderate to large size with skull architecture generally resembling that of *Potamochoerus* in early forms, but zygoma expanded laterally and drooping, especially in the male. Male canines resemble those of *Hylochoerus* in structure and cross-section, but relatively shorter and stouter; female canines much smaller than in the male and primitively rooted in some species. Cheek teeth resemble those of *Sus* or *Potamochoerus* in general structure but molars higher crowned and have lateral columns that are distinct and well separated. Talon of third molar tends to become more developed than in *Sus scrofa* or *Potamochoerus porcus*, exceeding the length of the main body of the crown in advanced species. Molar brachydont or moderately hypsodont, always strongly rooted. Little cement in more brachydont forms, abundant in hypsodont molars. Premolars rather more *Sus*-like than *Potamochoerus*-like; P^2 and P^3 triangular with well-developed protocone; P^4 equidimensional with a strong protocone and tendency toward the development of multituberculate and complex islands; P_4 has elevated anterior and posterior cingulum cusps and a double central cusp with the two elements displaced laterally relative to one another.

Remarks. *Kolpochoerus* is widely distributed in the later Pliocene and Pleistocene, ranging from South Africa to North Africa. This generic name has priority over *Mesochoerus*, which has been used in most of the literature. The type species is one of the most advanced in the genus.

Kolpochoerus afarensis sp. nov.*Diagnosis*

A suine about the size of the living bush pig, recognizable as *Kolpochoerus* by the structure of the zygomatic arch; differing from *Potamochoerus porcus* in possessing premolars that are less reduced and morphologically somewhat intermediate between premolars of bush pig and wild boar; P^1 normally, and P_1 sometimes retained in adult; lower canines verrucose; third molars relatively larger than in bush pig, tending to be more columnar and with smoother enamel on outer faces of main pillars; distinguished from *Kolpochoerus limnetes* by smaller size and by possession of only two pairs of fully developed laterals in the lower third molars.

Holotype. AL 147-10 in the Ethiopian National Museum, Addis Ababa, cranium with occiput and basicranium damaged, zygomatic arches and tips of premaxillae lost, P^3 - M^3 present on both sides in early wear; some lateral distortion and crushing of the cranium.

Locality: Hadar, Ethiopia

Hypodigm: SIDI HAKOMA. Type (SH-2); palate of juvenile with erupting canines, RP^1 , RM^{1-2} , LM^{1-2} intact, AL 224-3 (SH-1/2); maxilla fragment with RP^4 - M^2 , AL 222-4 (SH-1/3); maxilla fragment with RM^{2-3} , AL 218-1 (SH-1/3); isolated RM^3 , AL 200-13 (?SH-1); isolated RP^4 , AL 165-12 (SH-2). Mandibular ramus with base of canine, LP_4 , LM_{2-3} , roots LP_{1-3} , LM_1 , AL 109-1 (SH-2); mandibular ramus with roots of LP_3 , LM_1 broken, LP_4 , LM_{2-3} intact, AL 127-38 (SH-1); mandibular ramus with LM_2 , partial LM_3 , broken LP_4 - M_2 , AL 165-5 (SH-2); mandibular ramus with LM_{1-3} , AL 125-4 (SH-1/2); mandibular fragment with damaged LM_1 - LM_3 , AL 217-3 (SH-1/3); mandibular fragment with RdP_4 - M_2 , AL 248-3 (SH-2); mandibular fragment with LM_{1-2} , AL 214-1 (SH-4); mandibular fragment with LM_{2-3} , AL 148-101 (SH-1); mandibular fragments with M_1 : AL 147-24 (SH-2), AL 266-3 (SH-3), AL 277-8 (SH-2/3); mandibular fragments with M_3 : AL 131-4 (SH-2), AL 229-3 (SH-3), AL 199-2 (?SH-1), AL 251-34 (SHT), AL 255-1 (SH-1/2), AL 165-4 (SH-2), AL 327-19 (?SH-2), AL 325-9 (SH-4), AL 259-2 (SH-2); isolated M^3 , AL 233-3 (SH-4).

Referred Material: DENEN DORA. Partial cranium, lacking snout and occiput but with zygomatic arches, teeth broken, AL 154-34 (DD-2); pair of maxillae with LP^3 - M^2 , RP^4 - M^2 , AL 116-1 (DD-3); maxilla fragment with RP^3 - M^1 , AL 118-7 (DD-3); maxilla fragment with LP^4 - M^3 , AL 385-2B (DD-3); palate with P^4 - M^3 both sides and two fragments of mandible with M_{2-3} both sides, AL 56-16 (?DD-2/3); maxilla fragments: with P^4 - M^1 , AL 332-35 (DD-1), AL

358-12 (?DD-2); and M^{1-2} , AL 116-114 (DD-2); with M^{2-3} , AL 287-2 (DD-1); isolated LP^4 , AL 342-13 (DD-2); isolated M^1 , AL 116-42 (DD-2/3); isolated M^3 , AL 116-7 (DD-2), AL 201-1B (DD-2), AL 220-3 (DD-2). Incomplete mandible with roots of incisors and canine, LP_3 - M_3 , parts of right ramus with RM_{2-3} , AL 134-7 (DD-2); symphysis with base of left canine, AL 220-2 (DD-2/3); symphysis, right ramus with RM_{2-3} , anterior teeth broken, left mandibular fragment with LM_{2-3} , AL 321-10 (DD-3); mandibular ramus with LP_3 - M_3 , AL 385-2A (DD-3); mandibular ramus with RP_4 - M_3 , AL 168-13 (DD-2); symphysis fragment with RI_1 , LI_{1-2} , left ramus with LP_2 - M_3 , part right ramus with RP_{2-4} , AL 186-20 (DD-3); juvenile mandibular ramus with RP_4 - M_2 , M_3 in crypt, AL 185-20 (DD-3); mandibular fragments with LM_3 , RM_{1-3} , AL 116-60 (DD-3); mandibular ramus with RP_4 - M_3 , AL 116-15 (DD-3); mandibular ramus with RP_4 - M_3 , AL 183-44 (DD-3); mandibular fragment with LM_{1-3} , AL 169-16 (DD-2); mandibular fragments: with M_{2-3} , AL 379-3 (DD-2/3), AL 118-6 (DD-2/3), AL 291-10B (DD-3); with M_2 , AL 302-4 (DD-2), AL 169-19 (DD-2); with M_3 , AL 169-18 (DD-2), AL 187-12 (DD-3), AL 309-2 (DD-3).

KADA HADAR. Symphysis with four incisors and both canines, parts of rami with damaged LP_{3-4} , RP_3 , roots of RP_4 - M_2 , damaged RM_3 , AL 157-2 (KH-1); mandibular fragment with LP_3 - M_3 , roots LP_2 , AL 359-1 (KH-2); mandible fragment with RdP_4 , AL 367-1 (KH-2/3).

HADAR SOUTH. Maxilla fragments with LM^{2-3} , RM^3 , AL 273-1; mandible fragment with RdP_4 , RM_1 , and erupting RM_2 , AL 273-2.

UNCERTAIN HORIZON. Isolated M^3 , AL 246-5.

Description

The holotype comes from the middle part of the Sidi Hakoma member but unfortunately there are few other specimens of the upper dentition from this stratigraphic unit. The material from the Denen Dora unit seems to be a little larger, but the sample from the Sidi Hakoma is too small for it to be clear whether this is a real trend or a chance variation. The holotype lies near the lower limit for the entire sample but the morphology is characteristic. The samples for the lower dentition are bigger and show only a small trend towards larger size.

The Holotype

The holotype is an incomplete cranium from site AL 147, which also

furnished one isolated lower first molar. The cranium has lost the tip of the snout in front of the third incisors and also the upper part of the occiput, the occipital condyles, much of the auditory bullae and paramastoid processes, and most of the zygomatic arches. The specimen is deformed by pressure from the right side so that the midline of the skull is now almost directly above the left tooth row. In part, this has been accomplished by shearing of the maxilla and translocation of the snout and frontal area with relatively little actual distortion of the facial bones, although there is a mosaic of fracturing. The maxillary root of the right zygoma is partly preserved. There is also some backward compression of the skull. The palate is virtually intact and P³-M³ are present on both sides and almost complete, except for slight damage to RM¹ and LM³. The third molars are still erupting and the main pillars are just coming into wear, so that the dentition is in an almost ideal state. Measurements on the skull are necessarily a little speculative but some are given in Table 3, together with reliable measurements on the cheek teeth. The skull and teeth are illustrated in Plates 9 and 10 A.

TABLE 3

Measurements on Holotype Cranium of *Kolpochoerus afarensis* (in. mm)

AL 147-10							
Vertex length				+296 (c340-350e)			
Nasal breadth				c51			
Muzzle breadth				c55			
Ocular breadth				c75			
Frontal breadth				c110			
Posterior palatal breadth				33.5			
Posterior maxillary breadth				80.0			
Anterior palatal breadth				c41e			
	<i>length</i>	<i>breadth</i>	<i>height</i>		<i>length</i>	<i>breadth</i>	<i>height</i>
LP ³	14.7	9.8	10.5+	RP ³	14.0	10.0	11.5+
LP ⁴	12.7	13.6	10.0+	RP ⁴	12.8	13.2	9.5+
LM ¹ occlusal	18.6			RM ¹ occlusal	18.2		
basal	15.4	15.2	9.5+	basal	14.9	15.1	7.0+
LM ² occlusal	23.9	12.7		RM ² occlusal	24.1	13.0	
basal	21.0	19.2	12.5+	basal	21.4	19.4	12.5+
LM ³	34.3	20.2	16.0e	RM ³	33.9	19.6	16.0e+

In overall size and general morphology, the holotype cranium is very similar to the corresponding parts of the skull in *Sus scrofa* or *Potamochoerus porcus* and, in the absence of the zygomatic arches, might belong to either

genus. The nasals are moderately wide and appear to have been gently arched and to have curved smoothly into the side walls of the muzzle. The supraorbital foramina are about in line with the front of the orbits, and the canals leading from these are moderately deep. The orbits were well below the frontal surface, which was gently arched, and the frontal breadth is normal. The parietal constriction is narrow, being substantially less than the breadth of the snout, as is common in *Potamochoerus* whereas in *Sus* it is usually wider than the snout. The braincase probably bulged outwards below the parietal crest, as in the bush pig, but it is too crushed for this to be certain. The occiput was apparently narrow, but this area is too badly damaged for details to be seen. However, the squamous temporal bone was clearly broad at the base, with the external auditory meatus fairly low down, as in *Potamochoerus porcus*, not narrow and rather high as in *Sus scrofa*. The infraorbital foramina lie above the junction between P^4 and M^1 ; in *Sus scrofa* they are normally above P^4 and in *Potamochoerus porcus* above M^1 . The maxillary root of the zygoma has been pushed back into the orbit, but it would seem that there was only a moderately scooped area for the levator rostri attachments, not as deep as in typical *Sus*. The remnants of the auditory bullae and the paramastoid process appear normal.

The front of the premaxilla is broken through the sockets of the second left and third right incisors, but it is clear that the front of the snout was moderately long and narrow, much as in *Sus scrofa*. The left canine has been broken off with part of the bone, but the form of the flange is clearly seen and is small with an antero-posterior measurement of 15.3 mm and a transverse measurement of 8.9 mm. It is laterally more compressed than in a bush pig of the same age and like that of *Kolpochoerus limnetes*, but smaller. There is a good deal of distortion, but it would seem that the tusk pointed downwards much as in females of the wild boar and did not curve sideways even to the extent seen in modern bush pig females. There is a gap of approximately 10 mm between the front of the canine and the back of the socket for LI^3 , but crushing makes this measurement unreliable. About 1 cm behind the canine is the front of the anterior root of LP^2 , but it is not possible to determine whether P^1 was present or not, as this area is distorted and damaged. Judging by the roots, P^2 was about 12 mm long.

Of the cheek teeth, only P^3 - M^3 of both sides are known in the holotype. Measurements are given in Table 3 and length/breadth ratios are plotted in Fig. 8. The dimensions are closely comparable with those of *Sus scrofa*. Compared with *Potamochoerus porcus*, the third molars are larger than is usual, but the other teeth are similar in size. Morphologically, they are somewhat intermediate in character, but are less columnar than in *Kolpochoerus limnetes*.

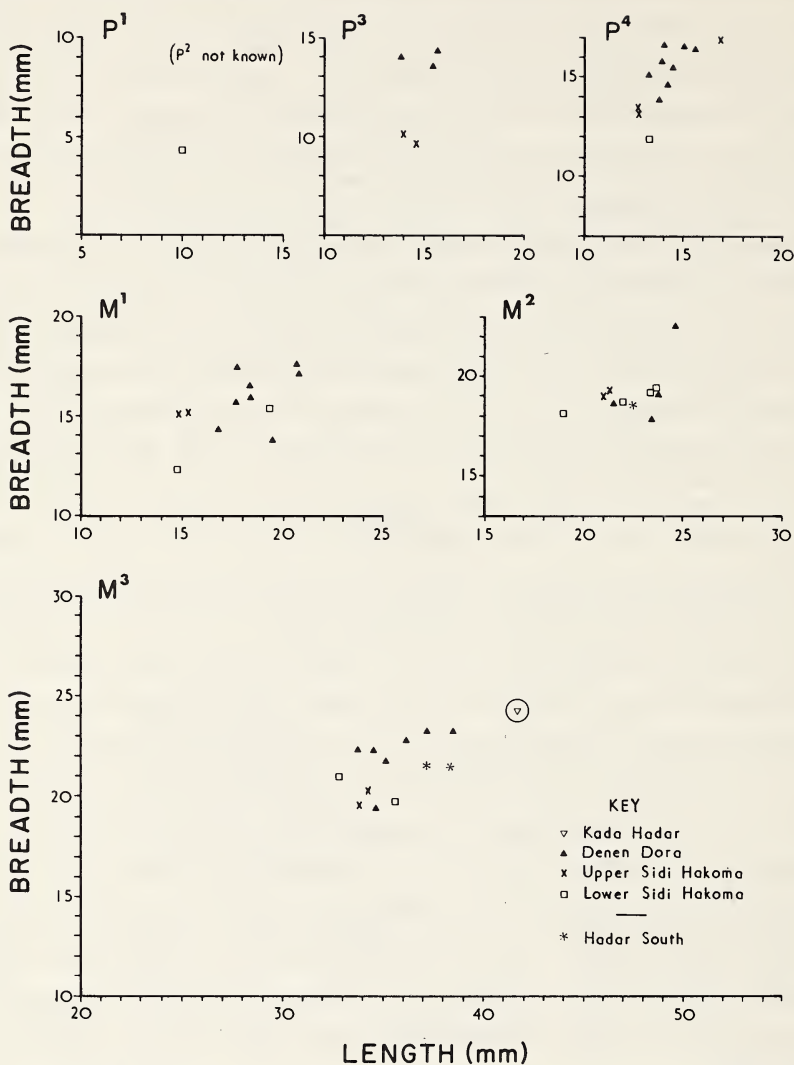
Kolpochoerus afarensis

Fig. 8. *Kolpochoerus afarensis*. Length-breadth measurements on upper cheek teeth. The circled measurement is for an unusually large specimen.

P³ is a sub-triangular tooth with the main cone (paracone) developed more strongly than in *Sus scrofa*, but not as robust as in typical bush pig. As in the latter, the anterior cingulum is not very well developed, but is strong enough for

an antero-internal fossa to develop in *Sus*-like fashion, though weaker. The posterior cingulum is also lower than in *Sus* and the postero-internal cusp (metacone) is small and rather isolated, but does not lead to the formation of a strong fovea in front of it, as is usual in the bush pig. The main cone is linked to the cingulum by well-developed ridges, making the tooth more sectorial than in bush pig at the same dental age. This structure is normal in *Kolpochoerus*.

P⁴ has the two outer main cusps (paracone and metacone) well developed and well separated, as in *Sus scrofa*, and the paracone is also somewhat larger than the metacone, whereas in the bush pig the two cones are roughly equal in size and are closer together. The protocone is large and antero-posteriorly elongate, and lacks any trace of the median spur that occurs typically in *Sus scrofa*, but not normally in the bush pig. In the former a wide and persistent fossa separates the paracone/metacone ridge from the protocone, but a narrow spur from the back part of the paracone juts into the fossa and tends to form two foveae, of which the anterior one is open to the front as the anterior cingulum does not block it. In the bush pig the fossa is narrow but the anterior cingulum extends partly around the protocone and blocks off the anterior fovea, while the posterior fovea is blocked by a strong cingulum that is tied to the back of the paracone. In the fossil, the paracone has a strong median spur that meets the front of the protocone and there are well developed cingulum cusps at the back of the crown that block the fossa. The result is the formation of a deep, wide, conical fovea that looks very like a volcanic crater. The anterior cingulum extends part way around the protocone, as in the bush pig, and a very small fovea is formed between it and the paracone and protocone. The cingulum development has resemblances to the bush pig condition, but the isolated protocone and very large fovea is more like the wide fossa in *Sus scrofa*. The distinctive structure of later *Kolpochoerus* is not yet developed.

M¹ and M² are very similar to the corresponding teeth of the wild boar and of the bush pig, which can be difficult to distinguish from one another. In *Sus scrofa* the enamel is thinner than in *Potamochoerus porcus*, and in the earlier stages of wear the clefts (or furrows of Hünemann, 1968) in the main pillars are wider and more open in *Sus* than in *Potamochoerus*, where they are hairline cracks. In the fossil teeth they conform to the latter rather than to the former. The successive pairs of laterals are more widely spaced than in *Sus scrofa*. The latter also tends to have the space between the first and second lateral columns on the inner (lingual) side filled by well-developed accessory basal pillars, which are less strongly formed in the bush pig. The fossil has only weak basal pillars on the inner side but does possess a single short basal pillar on the external (buccal) side between the well-spaced laterals; this sometimes occurs in second molars both in the wild boar and in the bush pig.

The third molars are relatively larger than in the bush pig but match closely in dimensions with the wild boar. There are two pairs of laterals and a single stout terminal pillar, as in both these living suids, although in both the talon may sometimes be more complex. As was the case with the first and second molars, the main pillars are smoother and less plicate than in *Sus scrofa*, and are also more distinctly separated and columnar than in the wild boar; indeed they are also rather simpler and better separated even than in living *Potamochoerus porcus*, presenting a less crowded appearance to the crown, as might be expected in a very early stage of *Kolpochoerus*.

Other cranial material

AL 224-3, from SH-1/2, is an important specimen as it provides information about the anterior cheek teeth. It is an incomplete palate, with a narrow rim of maxilla, and is broken across in front of the canines and through the palatal notch. The third molars are still completely in the crypt and the deciduous teeth have just been shed. The first and second molars are intact on both sides and the two canines are almost intact. RP^1 is preserved but LP^1 is broken off at the roots and the remaining premolars are represented only by the sockets. The root impressions of the last deciduous tooth on the right side are still visible and the distance from the front of P^1 to the front of M^1 on this side is about 5 mm longer than on the left side, so it may be assumed that the teeth will close up a little. There are no obvious gaps and it is considered that the arrangement was very much like that in *Sus scrofa*, with P^1 slightly separated from the canine, and the premolars just in mutual contact. Each of the P^1 's has a length of 9.8 mm and estimated measurements for the other premolars are approximately 14 mm for P^2 , 15 mm for P^3 and 14 mm for P^4 , an aggregate of 53 mm. The actual distance from the front of LP^1 to the front of LM^1 is 56.0 mm. This is greater than P^1-P^4 in *Sus scrofa* at the same stage of dental maturity, which ranged from 45 to 48 mm in three specimens available for comparison, but the difference is not great. In *Potamochoerus porcus*, P^1 is normally absent, but it is sometimes present in juveniles and is shed very early in life, at approximately the same time as the last milk tooth. In the fossil it is clear that P^1 is firmly rooted and it is expected that it would remain as a functioning tooth in the adult. In size and morphology it is almost identical with that in the living wild boar. In dimensions, the P^1 corresponds closely to P^2 in the bush pig, but the tooth is narrower and more bladelike in appearance; it is longer than the P^1 occasionally found in the bush pig in young animals. The M^1 and M^2 have the same characters as the corresponding teeth in the holotype cranium, but M^2 lacks the small external basal pillar between the laterals. The canines have only just emerged but the tip is already worn to a small facet about three quarters of a centimetre in length

(Plate 12 A). The anterior and posterior crests typical of a young canine are still visible and the morphology does not differ significantly from that of wild boar or bush pig at this stage of eruption.

The two maxillary fragments, AL 222-4, AL 218-1, and the isolated RM³, AL 200-13, confirm the general characters shown by the molars in the other specimens described above. The isolated RP⁴, AL 165-12, and the RP⁴ in the maxilla AL 222-4, do not exhibit the large craterlike fovea seen in the holotype and the pattern is more like that of the bush pig and early *Kolpochoerus limnetes*.

Mandible

The lower jaw is not very well known from the Sidi Hakoma member. The best specimen is AL 109-1, which is a left mandibular ramus broken through the canine socket, but retaining the left canine (Plate 12 B). The canine is verrucose and thus closer to the characteristic tusk of *Potamochoerus porcus* than to the scrofic one of the wild boar. The posterior face at the alveolar margin measures 15.0 mm, the internal face 19.7 mm, and the external face 17.5 mm. The three anterior premolars are all broken off at the roots, but their sizes can be estimated. P₁ lies about 7.5 mm behind the canine, as in *Sus*, and there is a gap of 25 mm between it and P₂, which must have been approximately 12–13 mm long, while P₃ had a length close to 15 or 15.5 mm. P₁ is thus about the size of the corresponding tooth in *Sus scrofa*, as also are P₂ and P₃. P₁ is about the same size as P₂ in the bush pig and both P₂ and P₃ are larger than in *Potamochoerus porcus*. In the fossil, P₄ is intact and is a little larger than in the bush pig, but close to the wild boar in size. The P₄ in *Sus scrofa* has a strong main cone consisting of two elements that are laterally displaced, so that there is a marked “kink” in the crest; in *Potamochoerus porcus* the protocone is stout and undivided. In the fossil there is a distinct deviation in the crest. The crest is also bladelike, as in *Sus scrofa*, and less expanded than in the bush pig; the internal buttress of later *Kolpochoerus* is not developed. The anterior and posterior cingula, although quite well developed, are not as high as in the wild boar. The tooth is thus more or less intermediate in character. In this jaw, the crown of M₁ is broken away but M₂ and M₃ are preserved. As was the case with the upper molars, they resemble the corresponding teeth of *Sus scrofa* and *Potamochoerus porcus* in structure but the pillars are less complexly folded than in the wild boar and are more columnar and better separated even than in the average bush pig. However, the third molar clearly has only two pairs of laterals and a stout median terminal pillar, flanked by accessory basal pillars, and is thus simpler than the specimen from Kaiso that Cooke and Coryndon (1970) named “*Sus*” *waylandi*, in which there are three pairs of laterals, as in

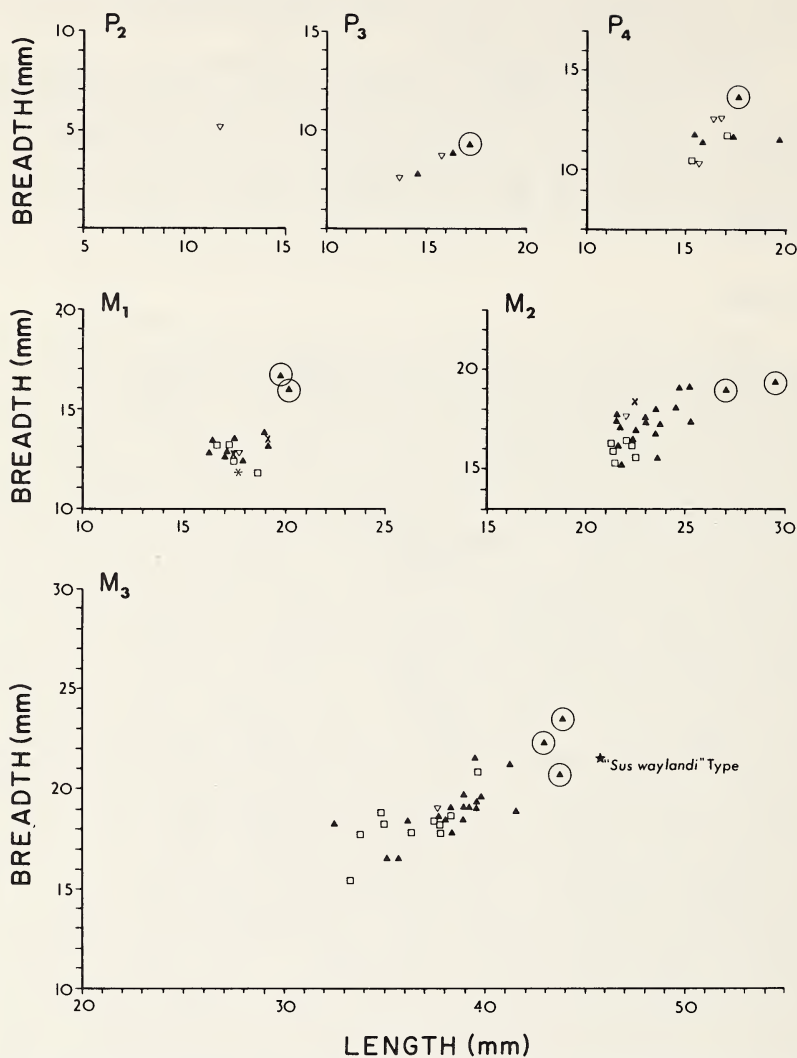
Kolpochoerus afarensis

Fig. 9. *Kolpochoerus afarensis*. Length-breadth measurements on lower cheek teeth. Key as in Figure 8. The type of "*Sus waylandi*" (now placed in *K. limnetes*) is also shown.

typical *Kolpochoerus limnetes* (to which *waylandi* is now referred).

The other mandibular fragments do not add significantly to the information given above, but serve to confirm that AL 109-1 is a fairly representative specimen. Only AL 127-38 has the P₄ preserved, and this is slightly smaller

than in AL 109-1, but morphologically similar. There are ten third molars from the Sidi Hakoma member, and these range in length from 33.5 mm to 39.8 mm, but all have essentially similar morphology. Length/breadth ratios are shown in Fig. 9.

Referred material

The Denen Dora member has yielded a substantial amount of material that can be referred without hesitation to the same species as that occurring in the Sidi Hakoma member. However, there are also found in the Denen Dora member four specimens that seem to be distinctly larger than the rest of the sample and also show slight differences in morphology. Although it is very likely that they are only variants, they will be discussed separately below. It is possible that they represent the beginning of an actual dichotomy. Under the circumstances, it has been thought best to restrict the hypodigm to the Sidi Hakoma sample. Many of the Denen Dora specimens contain parts that were not represented in the Sidi Hakoma material and thus warrant particular description. Length/breadth plots for all the referred cheek teeth are shown in Figs. 8 and 9.

AL 154-34 (DD-1/2) is a partial cranium, lacking the snout, the back of the braincase and basioccipital area, but apparently undistorted and having both zygomatic arches well preserved. It is illustrated in Plate 11. Most unfortunately, the M^2 and M^3 on both sides were in very advanced wear and have been damaged as well, so measurements on these are only approximate. RM^2 has a basal length of close to 23.5 mm and a breadth of 19.0 mm; LM^3 has a basal length of 38.5 mm and a breadth of 22.5, in good agreement with other material in better preservation. Both orbits are preserved and the frontal is broken across the braincase just behind them, so it is possible to measure the frontal breadth as close to 110 mm, which is virtually the same as the estimate for the holotype cranium. The interocular breadth is 85 mm, which is also close to that for the holotype, and the morphology of this part of the snout is very similar. There can be no reasonable doubt about the identity of the specimen as representing the same species as the holotype. The top of the orbit lies approximately 150 mm above the occlusal plane and the front of the orbit lies very slightly in front of the back of M^3 , as is also the case in *Potamochoerus porcus*, whereas in *Sus scrofa* (wild) and *Kolpochoerus limnetes* it is usually slightly behind the back of M^3 . The lateral profile is decidedly steeper than in wild *Sus scrofa*, or even *Sus verrucosus*, and is perhaps a little steeper than in *Potamochoerus porcus*, which it otherwise resembles closely. As in the bush pig, there are elevated ridges flanking the supraorbital canals, clearly seen as bumps in the profile. The flat naso-frontal area overhangs the maxilla, forming

a rather sharp edge above the scooped out area for the levator rostri muscles, as in the bush pig; the scooping is not quite as deep as in the wild boar. The origin of the depressor rostri, however, is relatively weak and shallow, as in *Sus scrofa* and *Kolpochoerus limnetes*, and not as deeply excavated as in the bush pig. The ridge between these two areas, which forms the maxillary root of the zygoma, is only moderately developed and rounded, unlike the strong sharp ridge of *Sus scrofa*. The root of the zygoma curves rapidly outwards until it is perpendicular to the skull axis and the jugal is greatly expanded laterally into large bosses that are rugose over much of the inflated area. Although there is a basic resemblance to the zygoma in old male animals of *Potamochoerus porcus*, there is less of a forward bulge and the lateral expansion is very typical of *Kolpochoerus limnetes*. There is also a resemblance to the zygomatic enlargement in the forest hog, *Hylochoerus meinertzhageni*, but in that species the zygomatic arches droop almost to the occlusal plane, whereas in the fossil and in the bush pig they lie at a much higher level. In the forest hog, the maxillary root of the zygoma is quite different; the broad parietal area is also quite unlike the braincase in the holotype. The bizygomatic breadth is 223 mm, which is greater than is usual in *Potamochoerus porcus*, for which 200 mm is rare and 175–180 mm more normal. The structure of the zygoma, coupled with the other morphological features already discussed, seem to place *afarensis* firmly in the genus *Kolpochoerus*, despite the existence of some more *Sus*-like characters and some *Potamochoerus* resemblances.

The upper dentition is well represented in the referred material, which is listed above, and includes two specimens in which P^3 is preserved, AL 116-1 (Plate 10 B) and AL 118-7 (DD-2/3). Both these P^3 's are more robust than in the holotype and correspondingly a little less like those of *Sus*, but larger than the somewhat reduced P^3 of *Potamochoerus porcus* (Fig. 8). The P^4 's are also larger than in the holotype, but not quite as large as in specimen AL 165-12 from the upper Sidi Hakoma member. The protocone blocks the fossa, as in the bush pig, but the paracone and metacone are more like those in *Sus scrofa* and *Kolpochoerus limnetes*. The third molars are also generally larger than the Sidi Hakoma sample, and there is a tendency for the molars to be more columnar and to have less secondary plication than in wild boar or in bush pig. In particular, the outer lateral pillars tend to become more rounded and smooth walled.

The best mandible is AL 134-7 (DD-2/3), comprising the symphysis and complete left ramus and also a fragment of the right ramus with RM_{2-3} . The canines are broken off at the alveolar margin and the incisors are badly broken. The left side of the jaw is damaged in front of P_3 and it is thus impossible to determine the size or form of P_2 . There is no sign of P_1 , or of a scar where it might have been (Plate 13 A/C). The general shape of the jaw and the sym-

physis are like those of the wild boar and the bush pig, but closer to the latter than the former. The canine flanges are more prominent than in the wild boar, and in profile the symphysis is flat or concave rather than slightly convex, as is the case with *Sus scrofa*. The back of the symphysis is about level with P_3 , whereas in *Sus scrofa* it is level with P_2 , but the small shelf developed in the bush pig for the insertions of the genioglossus and geniohyoideus muscles is not apparent. The mandibular ramus is thicker than in *Sus scrofa* and has a swollen appearance lateral to M_1 and M_2 , as in the forest hog and in *Kolpochoerus limnetes*. The incisors are broken but were generally like those of *Sus scrofa* or *Potamochoerus porcus*. The P_3 and P_4 are narrow cutting teeth, with P_3 very *Sus*-like. In P_4 (which is lying obliquely in the tooth row) the displacement of the central cusp is not as marked as in *Sus scrofa*, but it is also not as stout a tooth as in the bush pig. The first and second molars have less complex folding than in *Sus scrofa* and are more like those of the bush pig. However, the third molars are further simplified and the lateral columns are more distinct than in the bush pig and the outer walls of the main pillars are smoothly rounded, although the basic structure is still close to *Potamochoerus porcus* in respect of the number of columns present and in the limited development of the talonid.

Other material from the members DD and KH serves to confirm that AL 134-7 is a reasonably representative specimen. However, in a few of the third molars the large terminal pillar is accompanied by a second, smaller one. AL 157-2 (DD-3/KH-1) also includes the symphysis with broken incisors and canines, and this specimen also lacks any evidence for a lower P_1 in the diastema; the cheek teeth are too damaged to be informative. AL 116-60 (DD-2/3) is a right mandibular ramus with RM_{1-3} well preserved and a fragment of the left ramus with LM_3 . In this specimen the teeth are distinctly simpler in enamel folding, and the columnar laterals have a smooth, rounded external face, with thick enamel.

The Larger Specimens

Five specimens differ sufficiently in size from the other material to warrant special consideration. Three are from DD-1 and are: AL 287-1A, a left mandibular ramus with LP_3 - M_2 and part of LM_3 ; AL 296-1, a damaged mandible with the symphysis and some intact teeth; AL 325-8, a left mandibular ramus with LP_4 - M_2 . From DD-1/2 there is a fragment of mandible with LM_3 , AL 182-48, and from KH-1/2 a fragment of maxilla with RM^3 , AL 310-12. In Figs. 8 and 9 the plots for these specimens have been circled. The RM^3 lies just over two standard deviations from the mean for the remainder of the sample. The mean for the four lower third molars is almost exactly two standard deviations

distant from the mean for the remaining sample, but lies closely along the same regression line. Similar size differences apply to the other teeth, which is simply consistent with the fact that they belonged to larger-than-average individuals.

From a morphological point of view, the third molars in these specimens have thick enamel and the secondary fissures are merely thin cracks, while the main lateral pillars tend to be columnar and have smooth, rounded external faces. In all these respects, the teeth resemble those of *Kolpochoerus limnetes*, especially the material from the lowest members in the Omo sequence. However, the crown still consists of only two pairs of laterals and a single large median terminal pillar, whereas in *K. limnetes* there is normally a third lateral pillar on the lingual side in the uppers and on both sides in the lowers; in some early specimens, the third pair of laterals constitutes the terminal talonid, in place of the single median terminal pillar. Clearly these larger specimens point towards *K. limnetes*, while retaining the basic characteristics defined for the species *afarensis*. This is what one might expect if the latter is ancestral to *limnetes*, as seems very probable, and it is perhaps natural that the larger specimens should be most *limnetes*-like.

Discussion

The discovery of this small suid is of particular interest in furnishing a possible clue to the ancestry of the living bush pig, which is almost unknown as a fossil until the later Pleistocene. It may also provide a very reasonable ancestor for *Kolpochoerus limnetes*, whose primary origin has been uncertain. On purely dental grounds, the small Hadar suid might have been placed almost equally well in either *Sus* or *Potamochoerus*, although perhaps with a bias towards the latter, but the structure of the zygomatic arches is very different from that of *Sus* and so like that of *Kolpochoerus* that it is logical to assign it to the latter genus. There is a basic, but not exact, resemblance to the zygoma in the bush pig.

Consideration must be given to the possibility that *Kolpochoerus afarensis* is actually the direct ancestor of the living *P. porcus*, or even that it should be regarded merely as a fossil representative of that species. It has not been regarded here as a synonym of *P. porcus* because of the following considerations:

(a) the mutual relationships between the premolars and molars are different and have the same proportions as in *Sus scrofa*: P^1 is present in the adult, which is rare in bush pig, and P^1 and P^2 are virtually the same as in the wild boar, P^1 being almost as big as P^2 in the bush pig; M^3 is larger than in the bush

pig but the same size as in *Sus scrofa*. Similar relationships apply to the lower dentition.

(b) the premolar morphology is somewhat different from that of *Potamochoerus porcus*, not only in the rather more sectorial character of the second and third premolars, but also in the possession of a *Sus*-like displaced double crest in P_4 . The P_4 is more *Sus*-like and, despite the variability of this tooth encountered in living suids, the difference must be regarded as grounds for not placing the fossil into *Potamochoerus*.

(c) the molar teeth in the fossil tend to have thicker enamel and less folding than in the living bush pig. This would suggest some degree of specialization away from a bush-pig-like tooth rather than a truly ancestral type. However, the earliest specimens have molar teeth that are most like those of *P. porcus*, and thus early *Kolpochoerus afarensis* may well be very close to the branching point. Modification of the premolars would doubtless take place during the descent of *P. porcus*, leading to its present characteristics. It seems likely that the premolar characteristics that help to separate *Potamochoerus porcus* from *Sus* are not fully developed and it might be inferred that a still earlier ancestor might well be even more *Sus*-like in the premolar dentition. There is thus no particular reason to demand descent of *Potamochoerus* from *Pro-potamochoerus*.

As far as *Kolpochoerus limnetes* is concerned, *K. afarensis* seems to be a very suitable ancestor, with the degree of resemblance increasing in the higher stratigraphic horizons. It could be argued that it should therefore be placed in that species as a very early representative and that a distinction based on the number of lateral columns in the third molars is too arbitrary to be valid. Of course, in a more-or-less unbroken lineage of this type it is indeed difficult to draw a hard and fast boundary and any definition must be somewhat arbitrary. The literature teems with arguments about the problems involved in attempting to subdivide a continuously evolving lineage, especially in the absence of those frequent time gaps that often serve so conveniently to break up stratigraphic sequences into neat and manageable parcels. As W. S. McKerrow (1956) has pointed out, it is necessary "to realise that specific names in palaeontology are frequently only applicable to fixed points in a plexus of evolving organisms." Extension of a single species name to a morphologically changing complex over a long period of time avoids (or evades) the problem, but ceases to be useful when the end members in the lineage are so different that it is almost inconceivable that they would, or could, belong to the same biospecies if they had lived at the same time. As T. Neville George (1956) put it: "If a spade were always called a spade no doubt correlation would be greatly eased, though it might not be very exact if the spade were anything from a steam shovel to a

teaspoon." Palaeontological nomenclature should be stratigraphically useful as well as biologically reasonable. Accordingly, the present writer prefers to define *Kolpochoerus afarensis* as a species, recognizing that it will grade into *K. limnetes* and that some specimens may have to be dealt with by indicating their borderline character (easily done by use of the prefix *aff* with one of the species names). *K. afarensis* is thus regarded as close to the point of divergence of the *P. porcus* and *P. limnetes* lineages. Perhaps also belonging to this species are two third molars from Laetolil, Tanzania, described and figured by Dietrich (1942, figs. 150, 157) as *Potamochoerus* sp. cf. *major*.

DISCUSSION

The identifiable material assigned to each of the three species described here has been analysed in Table 4 to show the numbers of specimens from each stratigraphic submember, divided into upper and lower dentitions. Much fragmentary material has been omitted. On the right are shown the total numbers of specimens for each stratigraphic subdivision. It should be borne in mind that the units do not represent equal intervals of time and, accordingly, that the numbers do not represent original relative abundances. It is of interest to note that for each of the species, skulls and upper dentitions make up only one quarter to one third of the material, while the lower jaws and teeth are much better represented.

From a stratigraphic viewpoint, *Nyanzachoerus pattersoni* is almost confined to the Lower Sidi Hakoma member, with only three specimens from the Upper Sidi Hakoma. One isolated upper third molar from locality AL 134 is supposedly from DD-2/3 and if this is correct, then *N. pattersoni* still existed at that level, but it might be a derived or misplaced specimen. In the lower Sidi Hakoma member, *Notochoerus euilus* is almost as abundant as *Nyanzachoerus*, but *Kolpochoerus afarensis* is slightly less abundant, making up one quarter of the suid sample from this level. In the Denen Dora member, where *Nyanzachoerus* is effectively absent, *Notochoerus euilus* makes up 75% of the suid material and *Kolpochoerus afarensis* maintains its proportion of 25% of the suid sample. From the Kada Hadar there are too few suids for numbers to be significant, but both *Notochoerus euilus* and *Kolpochoerus afarensis* are represented.

As far as comparison with other sites is concerned, the *Nyanzachoerus pattersoni* material matches very closely with the sample from Kanapoi, where the age is estimated as close to 4.0 million years. The *Notochoerus euilus* material is generally similar to the large sample from the Usno Formation in the Omo area, which has an estimated age of close to 3.0 million years. However,

TABLE 4

Stratigraphic distribution of Hadar suid specimens
(individuals – upper and lower elements)

Stratigraphic Unit	<i>Nyanzachoerus pattersoni</i>		<i>Notochoerus euilus</i>		<i>Kolpochoerus afarensis</i>				Total
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	
KH-2/3	—	—	—	—	—	2	0	2	2
KH-2	—	—	1	—	—	—	1	0	1
KH-1/2	—	—	—	2	1	1	1	3	4
KH-1	—	—	—	1	—	1	0	2	2
DD-3/KH-1	—	—	1	2	—	1	1	3	4
DD-3	—	—	5	11	3	9	8	20	28
DD-2/3	1?	—	11	24	2	4	14	28	42
DD-2	—	1	11	25	7	6	18	32	50
DD-1/2	—	—	5	23	—	—	5	23	28
DD-1	—	—	1	9	2	4	3	13	16
SH-4/DD-1	—	—	3	2	—	—	3	2	5
SH-4	2	1	3	7	1	2	6	10	16
SH-3/4	—	1	—	2	—	—	0	3	3
SH-3	1	1	2	2	—	2	3	5	8
SH-2/3	—	—	1	6	—	1	1	17	8
SH-2	6	9	—	4	2	7	8	20	28
SH-1/3	—	14	1	7	3	4	4	25	29
SH-1	—	4	1	5	1	3	2	12	14
Basal	—	1	—	—	—	1	0	2	2
HS	—	1	—	—	1	1	1	1	2
Uncertain	—	—	1	4	—	—	2	4	6
Totals	10	32	47	136	24	49	81	217	298
As % of species	23.8	76.2	25.7	74.3	32.9	67.1	27.2	72.8	
Summary									
Kada Hadar	0	0	2	5	1	3	3	10	13
Denen Dora	1?	1	33	92	14	23	48	116	164
Upper Sidi									
Hakoma	3	3	8	13	1	4	12	20	32
Lower Sidi									
Hakoma	6	27	3	22	6	15	15	64	79
Miscellaneous	0	1	1	4	2	2	3	7	10
As % of									
Grand	3.4	10.7	15.8	45.6	8.1	16.4	27.2	72.8	
Total	14.1%		61.4%		24.5%		100.0%		

the Hadar material from the Sidi Hakoma member seems to be a little more "primitive" and closer to its presumed ancestor, *Nyanzachoerus jaegeri*. An age for the Sidi Hakoma member of 3.0–3.5 million years would give a better fit than the 2.9–3.0 m. y. age presently obtained from the basalt, while an age close to 3.0 million years for the Denen Dora member would be best in line with the stage of evolution of the *Notochoerus euilus* material. Thus, the suid evidence confirms in general the age provisionally assigned to the Hadar Formation but suggests that the lower part may be a little older than the present radiometric determinations indicate.

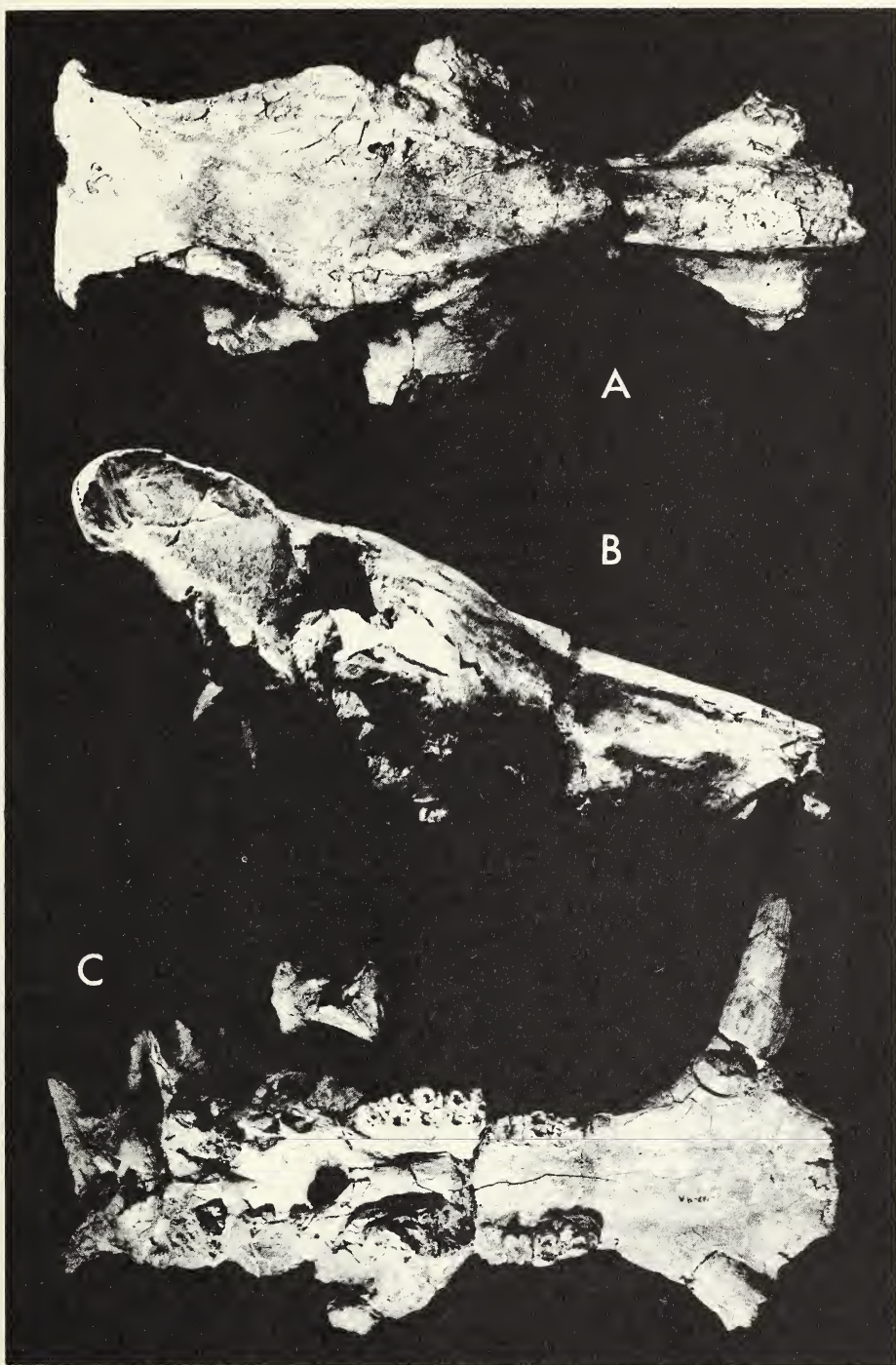


Plate 1. *Nyanzachoerus pattersoni*, male AL 137-4, dorsal (A), right lateral (B) and palatal views. One-fifth natural size.

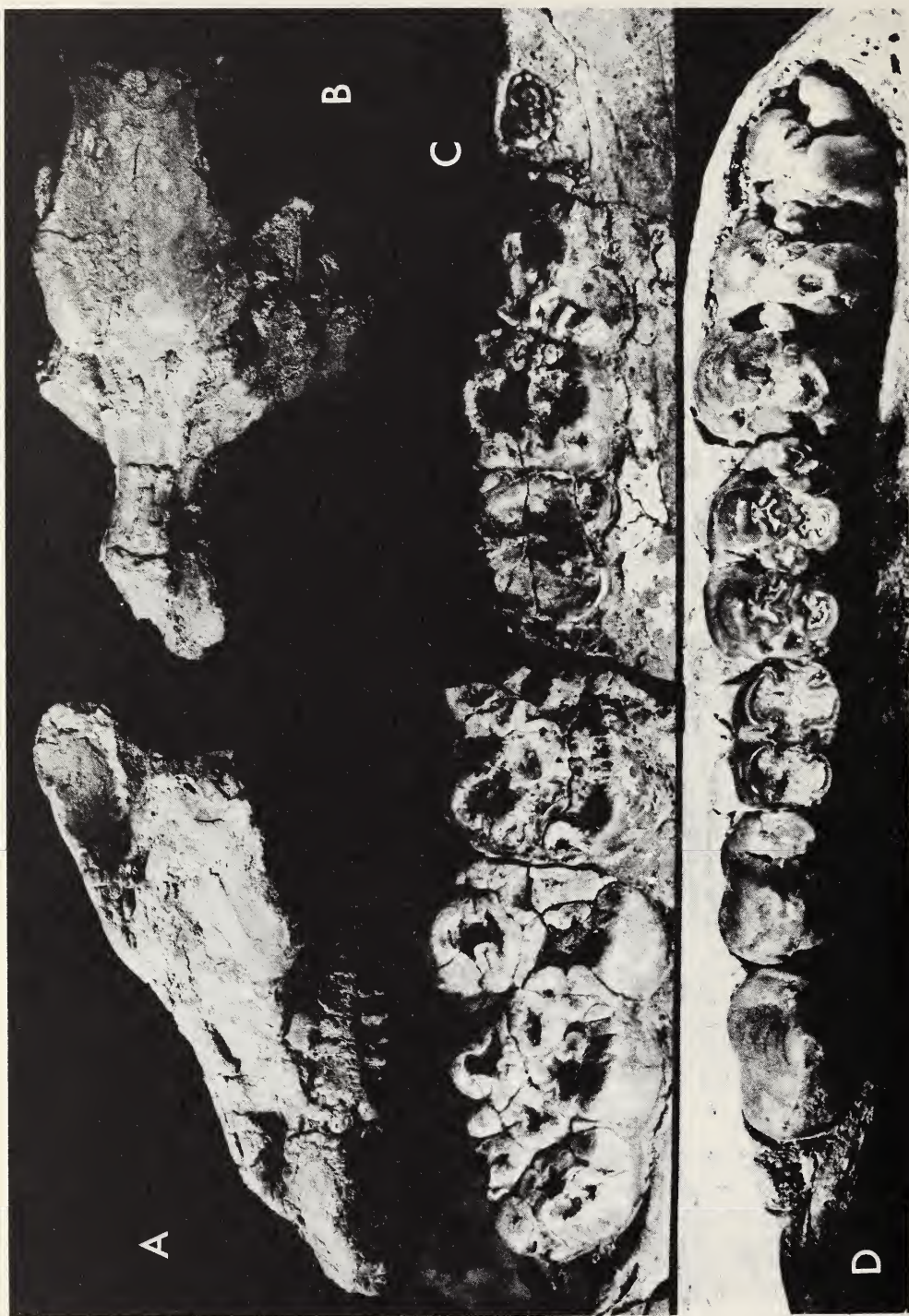


Plate 2. *Nyanzachoerus pattersoni*. A, left lateral, and B, dorsal, views of female, AL 107-13, one-fifth natural size. C, right upper cheek teeth of male AL 137-4 (with dislocation seen in plate 1 B removed photographically), natural size. D, left lower cheek teeth, AL 126-8, natural size.

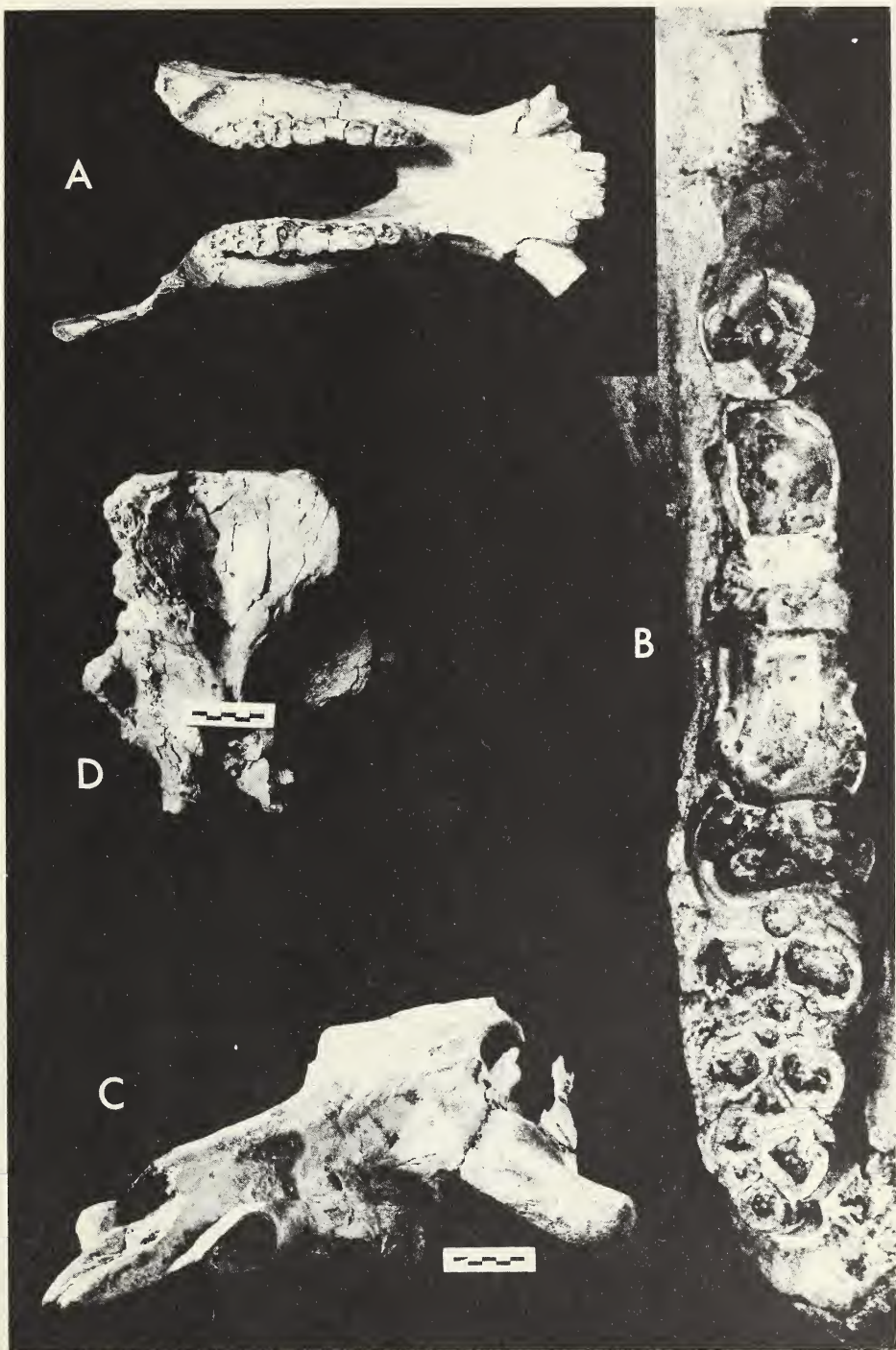


Plate 3. *Nyanzachoerus pattersoni*, AL 218-2: A, mandible of old individual, one-fifth natural size; and B, right lower cheek teeth, natural size. *Notochoerus euilus*, AL 172-1: C, oblique view to show the form of the zygomatic protuberances; D, occiput, one-fifth natural size.



Plate 4. *Notochoerus euilus*, AL 172-1, dorsal (A), palatal (B), and right lateral (C) views, one-fifth natural size.



Plate 5. *Notochoerus euilus*, AL 172-1, palate and cheek teeth on both sides. Natural size.



Plate 6. *Notochoerus eulius*, upper right cheek teeth. A, very young adult, AL 108-3; B, AL 167-15, adult with RP⁴ damaged; and C, intact LP⁴ showing the posterior cingulum development; D, AI 116-93. All natural size.



Plate 7. *Notochoerus euilus*, AL 116-28. A, mandible with both incisors, one-fifth natural size; B, cheek teeth of both sides, natural size.

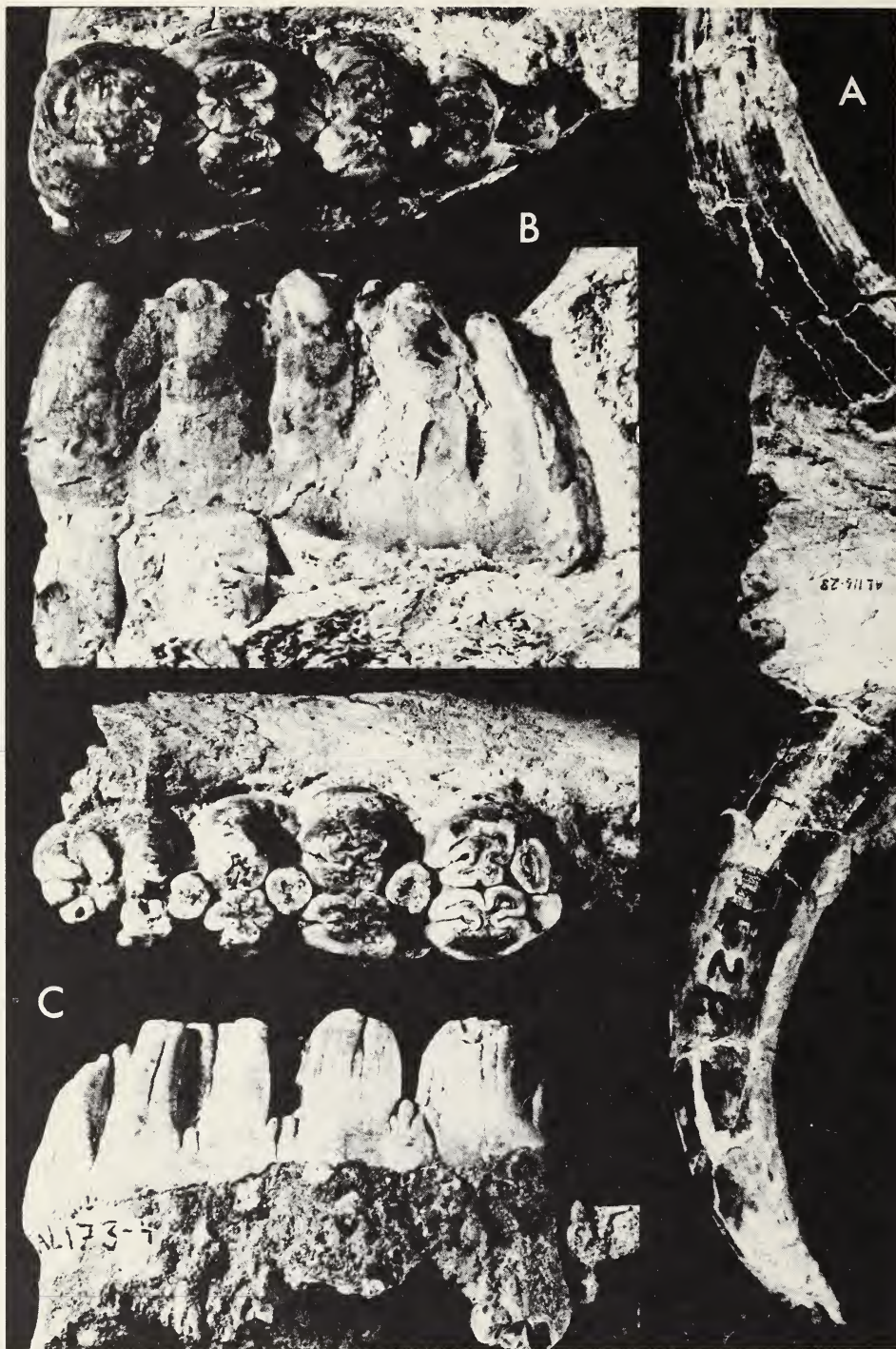


Plate 8. *Notochoerus eulius*. A, anterior border of symphysis with LI_{2-3} intact and roots of other incisors, one-half natural size. B, AL 122-5, LM_3 in early wear, occlusal and outer lateral views, natural size; C, AL 173-4, LM_3 in moderate wear, inner lateral and occlusal views, natural size.



Plate 9. *Kolpochoerus afarensis*, Holotype, AL 147-10, left lateral (A) and palatal (B) views, one-third natural size.



Plate 10. *Kolpochoerus afarensis*. A, palate and cheek teeth of Holotype, AL 147-10. B, palate with P³-M² on both sides, AL 116-1. Natural size.

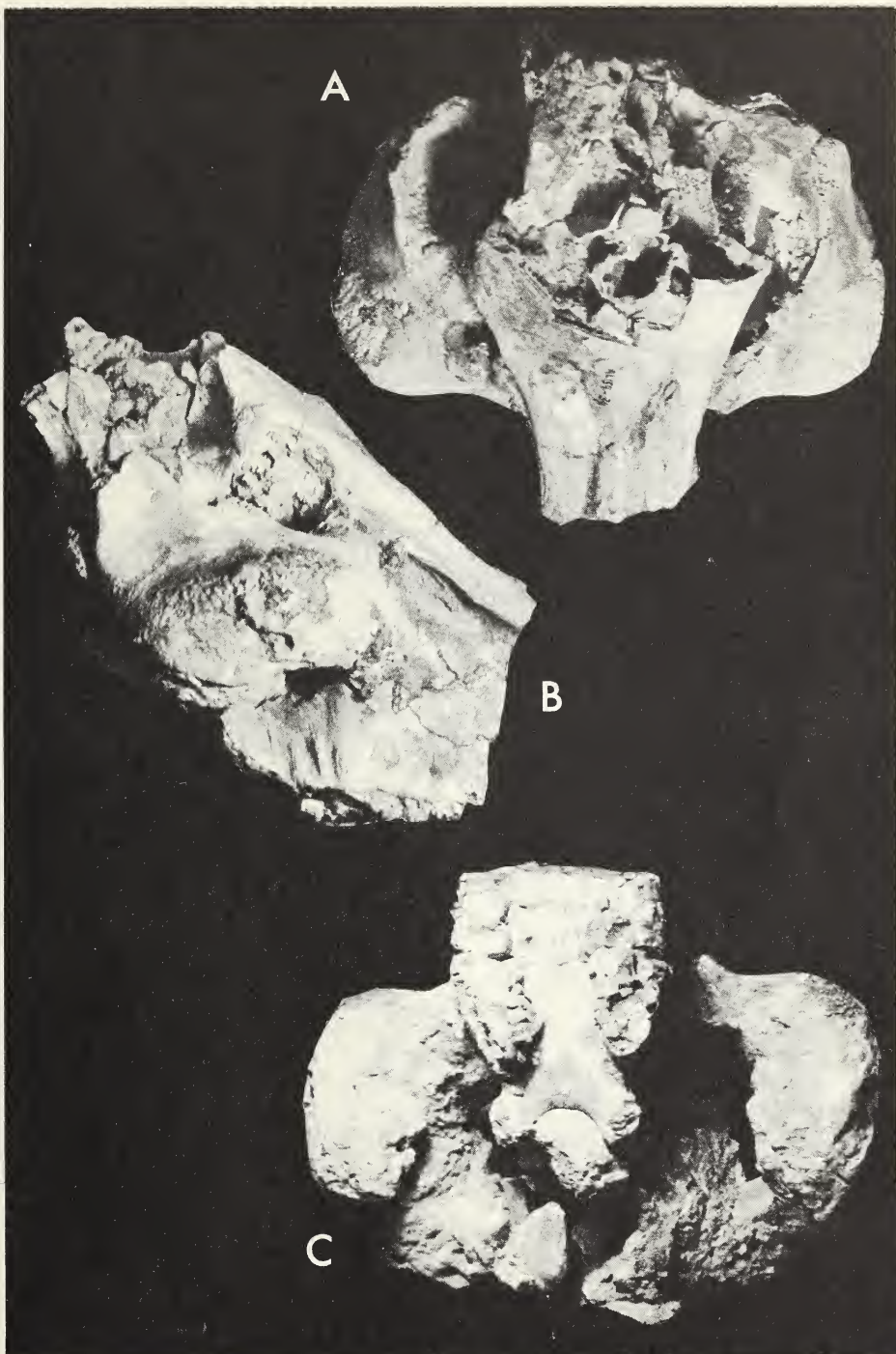


Plate 11. *Kolpochoerus afarensis*. AL 154-34, partial cranium of old individual, dorsal (A), right lateral (B), and palatal (C) views. One-third natural size.



Plate 12. *Kolpochoerus afarensis*. A, palate of juvenile, AL 224-3, with canines erupting, RP¹ and M¹⁻² on both sides; B, AL 109-1, left mandibular ramus with broken canine, socket of LP₁ near canine, roots of LP₂₋₃ and LM₁, LP₄, LM₂₋₃ intact. All natural size.

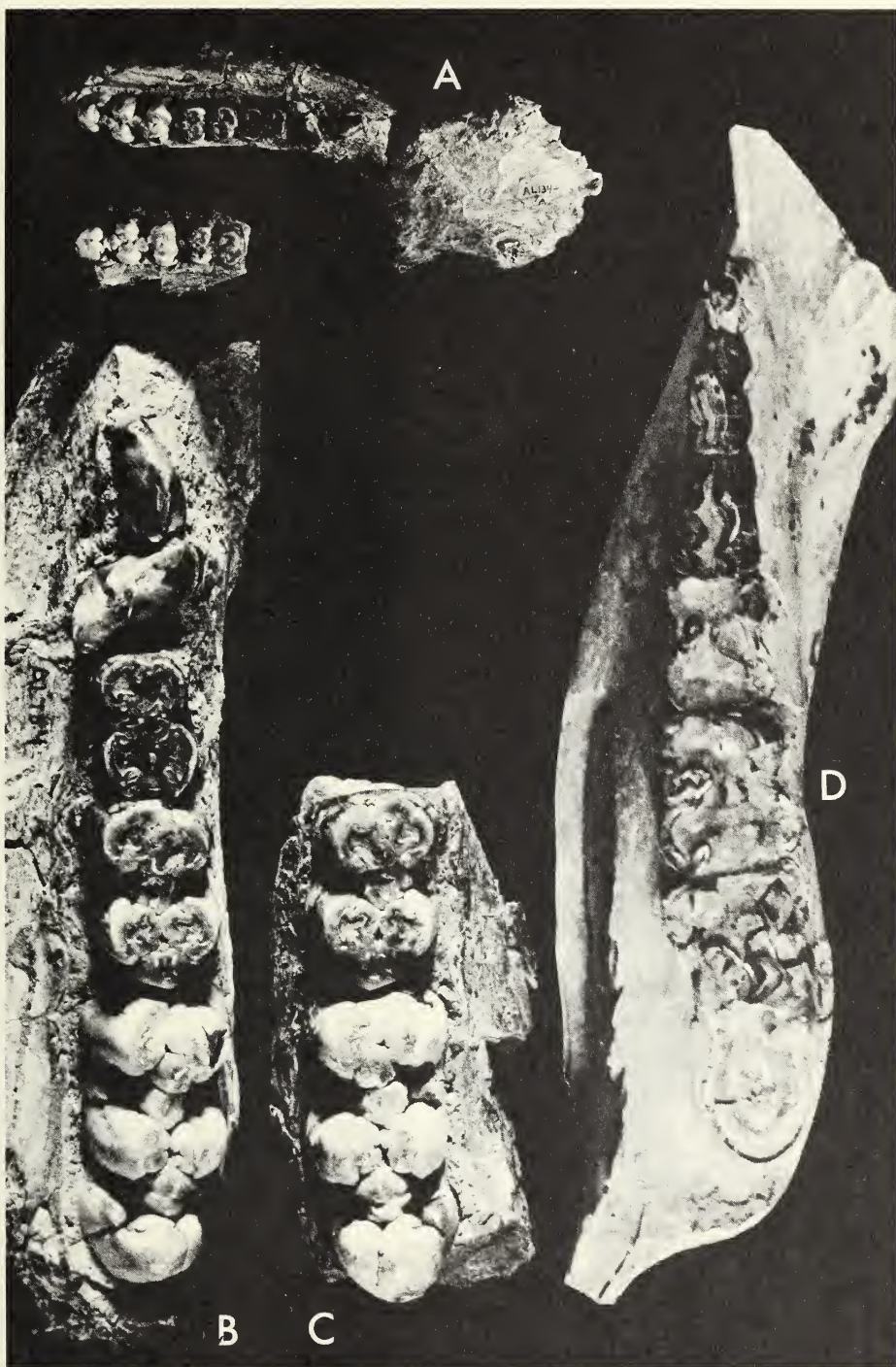
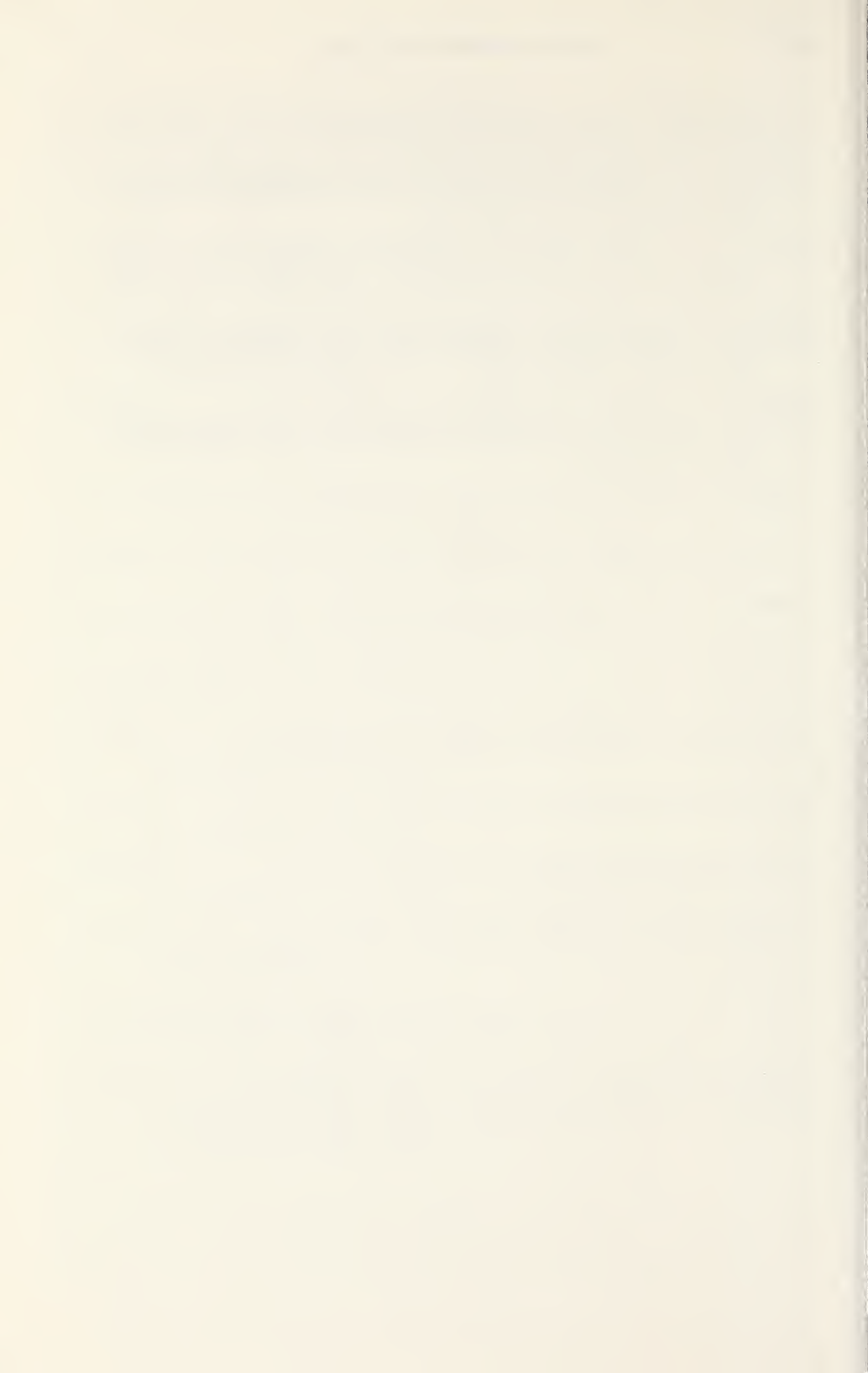


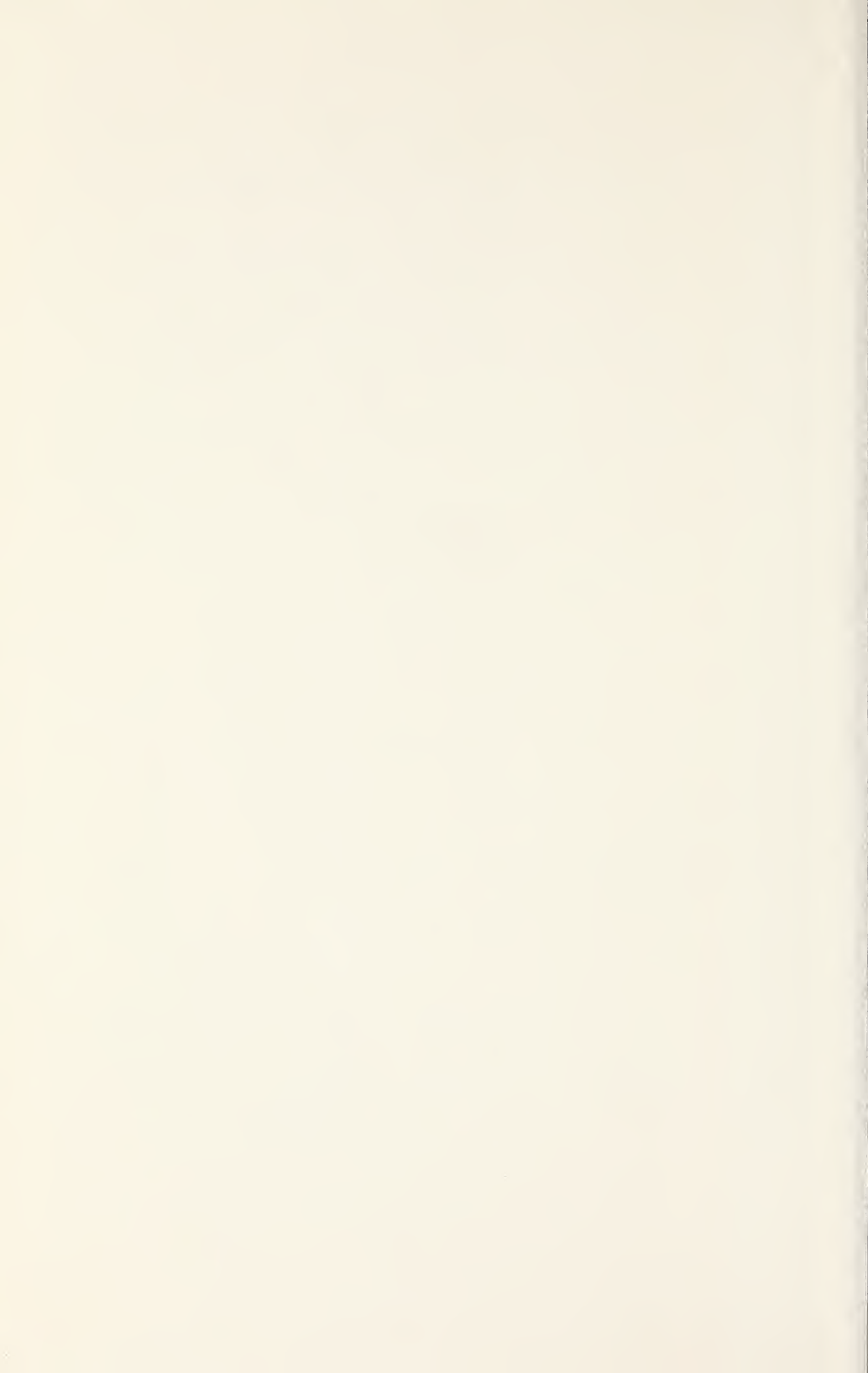
Plate 13. *Kolpochoerus afarensis*. A, AL 134-7, incomplete mandible with good symphysis, one-fifth natural size; B, left cheek teeth of A, showing the oblique LP₄, and C, right M₂₋₃, natural size; D, AL 186-20, left mandibular ramus with good LP₂₋₄ and well-worn LM₁₋₃, natural size.

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